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COVER ILLUSTRATIONS: *Lycaena heteronea clara* female necturing on *Eriogonum fasiculatum.*

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Cover Illustration: *Uraba lugens*, last instar larva showing retention of head capsules of all prior instars. McFarland, pages 209-217.

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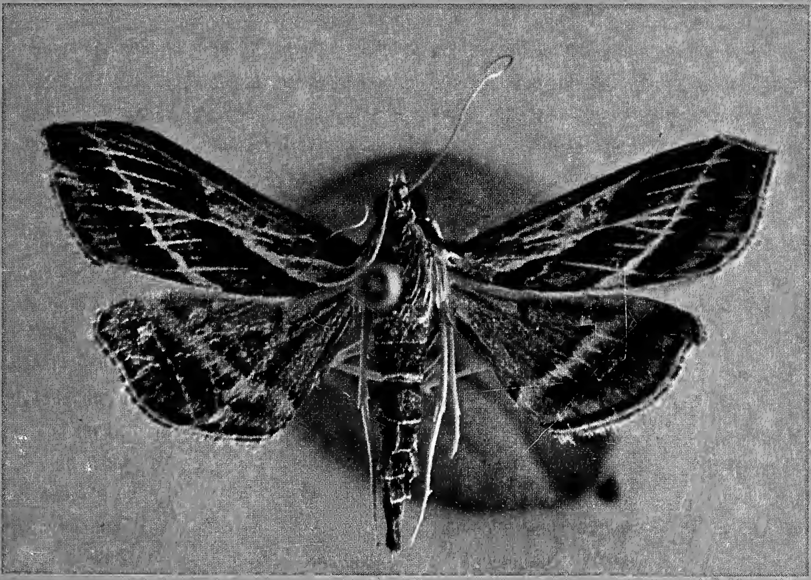

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WEATHER AND THE LABILITY OF BREEDING POPULATIONS OF THE CHECKERED WHITE BUTTERFLY, *PIERIS PROTODICE* BOISDUVAL and LeCONTE

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ABSTRACT. In the Sacramento Valley and Sierra Nevada of northern California, *Pieris protodice* populations experience frequent colonizations and extinctions. Overwintering success and colonization rate are roughly correlated with weather. "Permanent" populations exist in local areas of dredge tailings habitat; these are the sources of each year's first colonizers. The Ehrlich and Birch "mosaic" model of population regulation appears to be a good description of the dynamics of *P. protodice* populations.

INTRODUCTION

Two controversial areas of theoretical population biology —island biogeography (MacArthur and Wilson, 1967) and group selection (Wynne-Edwards, 1962; Williams, 1966) — revolve to a substantial extent on the question: "How permanent are natural populations of plants and animals?" A high turnover of local populations is theoretically conducive to rapid evolution and speciation. Defensive adaptations of plants and host-selection patterns in herbivorous insects have been linked to rates of population turnover (Feeny, 1975). For all these reasons data on the permanence or impermanence of populations are highly desirable, but unfortunately scarce in many otherwise well-studied groups of organisms.

The butterflies have received a tremendous amount of attention from population biologists, but population-turnover data are few. Ehrlich *et al.* (1975) summarized 15 years of tracking the Jasper Ridge population of *Euphydryas editha* Boisduval (Nymphalidae). During this time local subpopulations repeatedly waxed and waned sometimes asynchronously, with at least one extinction. Ehrlich *et al.* (1972) described the impact of anomalous weather on various organisms at Gothic, Gunnison County, Colorado: one of the casualties of an unseasonal snowstorm was a population of *Glaucopsyche lygdamus* Doubleday (Lycaenidae) which was apparently eradicated. The ups and downs of British Lepidoptera are chronicled in the *Entomologist's Record,* and some are summarized by Ford (1957).

Against this evidence for population lability there are isolated colonies of butterflies which have been observed by generations of collectors and whose "stability" is proverbial. In the United States a good example is the Coy Glen population of *Asterocampa clyton* Boisduval and LeConte (Nymphalidae), which has seemingly persisted for over 35 years in central New York near the species boundary (Shapiro, 1974c). Bonafide relict populations on mountaintops, in peat bogs, and on sand barrens obviously demonstrate long-term persistence (thousands of generations) since the probability of recolonization under present ecological and climatic conditions is so low.

The distinction between high- and low-turnover populations may correspond to that between r- and K-selected species (MacArthur and Wilson, 1967; Force, 1974). The relative importance of density-dependent and density-independent controls is thought by many authors to vary between them. Ehrlich and Birch (1967) proposed a "mosaic" model of population regulation which incorporates both types of control. The essential features of this model have been summarized concisely by Ricklefs (1973: p. 475):

> They suggested that populations should be thought of as consisting of a mosiac of numerous (sub) populations that receive occasional immigrants from other areas but are otherwise independent. If a local population became extinct by chance fluctuations in size, it could be re-established by colonization from surrounding populations . . . while extinction may occur by chance, the colonizing ability . . . depends on how many areas of habitat are free of individuals. When the population is sparse, many local areas are available for recolonization; when it is dense, few areas are unoccupied . . . the tendency to increase through colonization of new areas is density-dependent.

This model appears to simulate processes which are thought to occur in many butterfly populations. Its applicability to the dynamics of populations of the Checkered White, *Pieris protodice* Boisduval and LeConte (Pieridae), is described below.

CHARACTERISTICS OF THE CHECKERED WHITE

Pieris protodice is a common butterfly over most of the United States except New England and the Pacific Northwest (Shapiro, 1976). It is usually found in disturbed habitats, including desert washes, ocean beaches, and urban vacant lots. Over most of its range it occurs at low to moderate altitudes; its upslope and northward restrictions imply climatic intolerance. Its host plants are weedy Cruciferae, native and introduced, annual and perennial. Over most of its range it prefers species of *Lepidium* where available. In lowland California its most important host is *Brassica geniculata* (Desf.) Ball. It is multivoltine everywhere in its range, with up to six generations a year in lowland California and two to three in the mid-Sierra Nevada at 1500-2000 m. (Shapiro, unpub.)

The Checkered White has some reputation as a fugitive species; the unpredictability of its occurrence was noted by Clark and Clark (1951), Rawson (1945), and Maeki and Remington (1960). Tilden (1965) says it "may be found most of the year . . . in every back yard and farm lot" in the San Francisco Bay area; but in many years it cannot be found in the Bay area at all. The California literature gives a misleading impression that *P. protodice* is ubiquitous and always common. Actually it has probably been taken throughout the state, but is often absent from entire counties for entire years or parts of years.

Since 1972 sampling has been done on a year-round, weekly to biweekly basis at selected sites in Yolo, Solano, and Sacramento Counties, northern California, at a constant level of effort as part of a long-term community phenology study (Shapiro, 1975a). A by-product of this sampling has been detailed documentation of the spatial and temporal distribution of the 55-odd species in the breeding butterfly fauna of the Valley. The fauna is mostly multivoltine and decidedly weedy (Shapiro, 1974a) and many of the species show dramatic year-to-year population fluctuations, but none so dramatic as that of the Checkered White. Similar patterns occur in *Lerodea eufala* Edwards (Hesperiidae), *Brephidium exilis* Boisduval (Lycaenidae), and *Precis coenia* Hübner (Nymphalidae), as well as others, but their biology is less well known.

THE CHECKERED WHITE IN THE VALLEY

The Checkered White has been taken throughout the entire length of the Sacramento Valley, but it occurs reliably and overwinters predictably only on the dredge tailings along the east side of the Valley. This unnatural habitat dates to early in this century when "large gold dredgers floated in artificial ponds in broad stream valleys and flat lands bordering the western foothills (of the Sierra Nevada) to excavate the gravel below the surface. When the 'washings' emerged from the dredgers (after separating out the gold), the soil particles went to the bottom and huge mounds of large creekworn boulders were piled on the surface of the land . . . Several decades are required for enough air-borne soil to accumulate on the boulder heaps so that plants and trees can take root" (Storer and Usinger, 1971). The resulting landscape has provided a refuge for native plants and animals in a largely urbanized and agriculturalized region. The restriction of *Pieris protodice* as a permanent resident is not, however, due to lack of suitable breeding habitat elsewhere. Its host, *Brassica geniculata,* is very common on the tailings but also occurs widely elsewhere on sandy loam soils. In most years breeding colonies of the butterfly may be found far from the dredge tailings, on *B. geniculata* and other Crucifers, but they do not persist into a second season. As discussed below, most local extinctions appear to occur over winter, suggesting that the diapausing pupa is subject to the "key" mortality factor. Although larvae can be found at almost any time in exceptionally mild winters, normally overwintering occurs only in the pupal state. Its facultative diapause, under the control of larval photoperiod and temperature exposure, is of low intensity: diapausing pupae (induced under 10L:14D with day and night temperatures of 17.5°C and 10°C) removed to 25°C on their seventh day generally eclose in 4-9 weeks. As Tauber and Tauber (1976) have shown, diapause terminates in midwinter in most insect populations. For such a weak diapauser near the northern edge of its range, vulnerability to weather-induced winterkill may be very great.

A CAVEAT

This paper does not pretend to be a rigorous demonstration of causation, or even of statistical correlation, between weather and population levels. It is, rather, a qualitative presentation of a *plausible* pattern of causation for the observed facts, i.e., the presence or absence of the Checkered White at the study sites throughout the years 1972 through 1977, and the much-publicized drastic fluctuations in northern California weather during that period, which includes the 1975-77 drought. Of the populations discussed here, precise estimates of density, based on mark-release-recapture studies, are available only for two, and not in all years. The narrative which follows presents trends in abundance based on eyeball estimates — essentially and inescapably subjective, but made as validly comparable as possible by an experienced observer following consistent procedures. Because all butterfly species present were being monitored phenologically at each site, the effort involved in tracking population levels at the level of rigor applied to Ehrlich's univoltine, circumscribed *Euphydryas* was out of the question.

Identification of the relevant weather elements is also difficult. When numerical population estimates are available, multiple regression and correlation techniques can be applied to identify those weather elements most useful in prediction. First-flight data do not lend themselves to such treatment unless very long runs of data are available. Commonly in ecological studies, weather data from the nearest recording station of the government meteorological service, or from a limited-scope station set up at or near the study site in a conventional instrument shelter by the investigator, are reported and create an illusion of rigor. The most meaningful data for studies of overwinter survival of butterfly pupae or reproductive success of adults involve sophisticated measurements of aspects of ground-level and boundary-layer microclimatology. Table 1, containing an abstract of climatological data for one location within the study area (Executive Airport, Sacramento, NWS recording station), gives the sort of data actually available. Although trends are obvious to residents, and to climatologists having access to data from many stations, idiosyncratic aspects of local data not uncommonly obscure them when one or a few stations are used. Data of this sort are thus simultaneously too coarse-grained (relative to microclimate) and too fine-grained (relative to local departures from regional patterns) for confident use. The Sacramento data are provided to convey a general picture of weather in the study area, but because they are inherently inadequate to do so a narrative summary for the three-county area is coupled with the butterfly observations. West Coast rainfall-pressure patterns throughout the period are discussed regularly in the *Monthly Weather Review.*

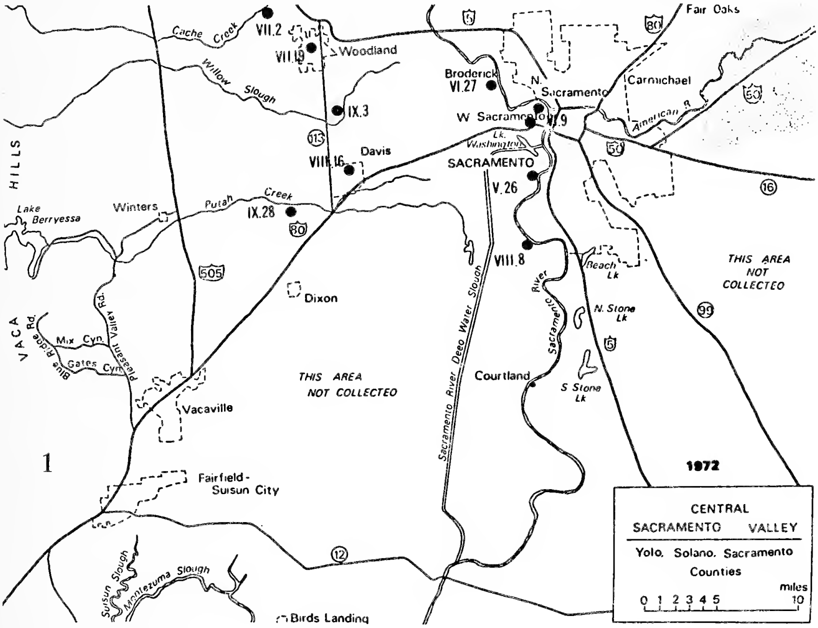
Neither monthly temperature or rainfall data, nor their deviations from the arbitrarily selected 30-year means, directly affect butterfly survival except in rare extreme cases. Outright thermal lethality is almost never observed. The day-to-day distribution of temperature, rainfall, dew, cloudiness and wind determines survival and reproductive success and growth rate, operating at and near ground level, and these aspects of "butterfly weather" are very difficult to extract from climatological data summaries. Although no specific data are available for *Pieris,* pupal death due to bacterial and fungal parasites is believed to increase dramatically under mild (7°C) and wet winter conditions. A variety of *sequences* of individually innocuous events can be lethal to post-diapause pharate adults (uneclosed adults within the pupal case, ed.), just as rain or frost on two or three critical days can prevent effective pollination of a fruit-tree crop — a critical event not readily apparent from columns of means and deviations. With adequate numerical population estimates and microclimatic data whose collection has been imaginatively designed in advance, more rigorous assessments of the role of different weather elements in insect population dynamics are thoroughly feasible. The overall pattern of how, say Checkered White populations behave — as presented here — is *not,* however, inferable from the dynamics of any single, local population, no matter how well quantitated.

HISTORY IN THE VALLEY, 1972-77

Figures 1 - 6 show the first dates when *Pieris protodice* was recorded at sites away from the dredge tailings from 1972-1977. It is immediately clear that there is great year-to-year fluctuation in first-flight dates. Since *P. protodice* is obligately multivoltine, it would appear that (from the frequency of absences) a high turnover rate of local populations must exist.

The autumn of 1971 was prolonged, warm, clear, and dry; the winter, mild and dry. *Pieris protodice* first appeared in western Sacramento and adjacent Yolo County in late May - early June 1972, with no evidence of overwintering in these locations. The summer was hot and dry. Despite an early start and gener-

Figures 1 - 6. First dates of capture of *P. protodice* at sampling stations in the Sacramento Valley from 1972 through 1977. Dredge tailings (Rancho Cordova) are stippled. 1 mile = 1.61 km.



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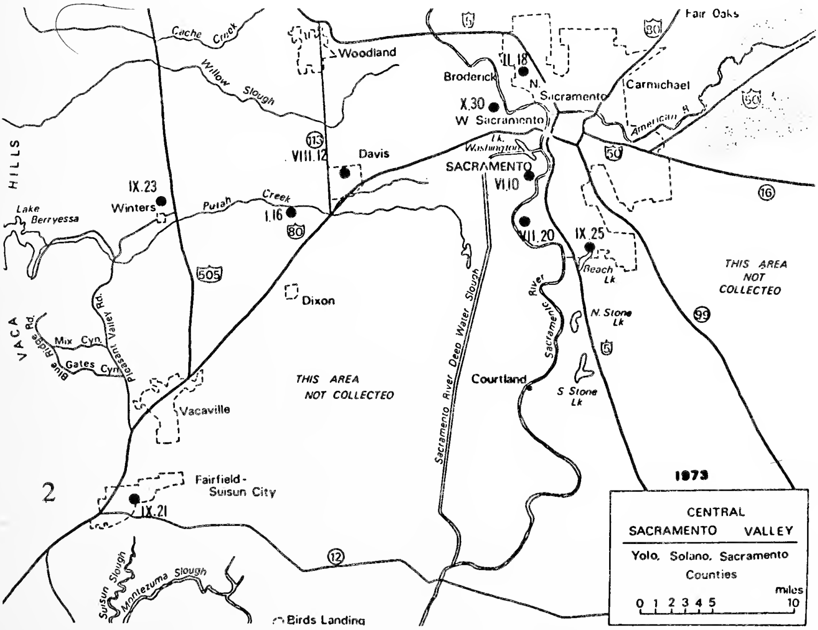

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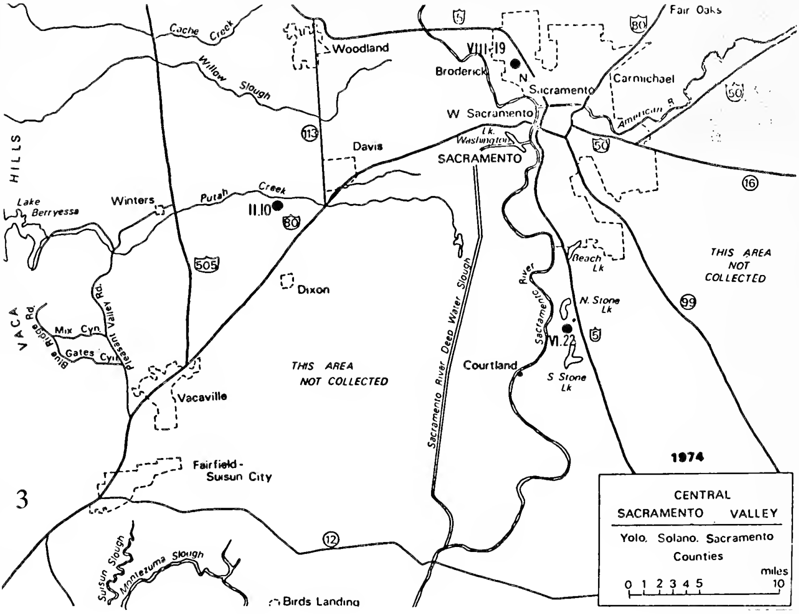
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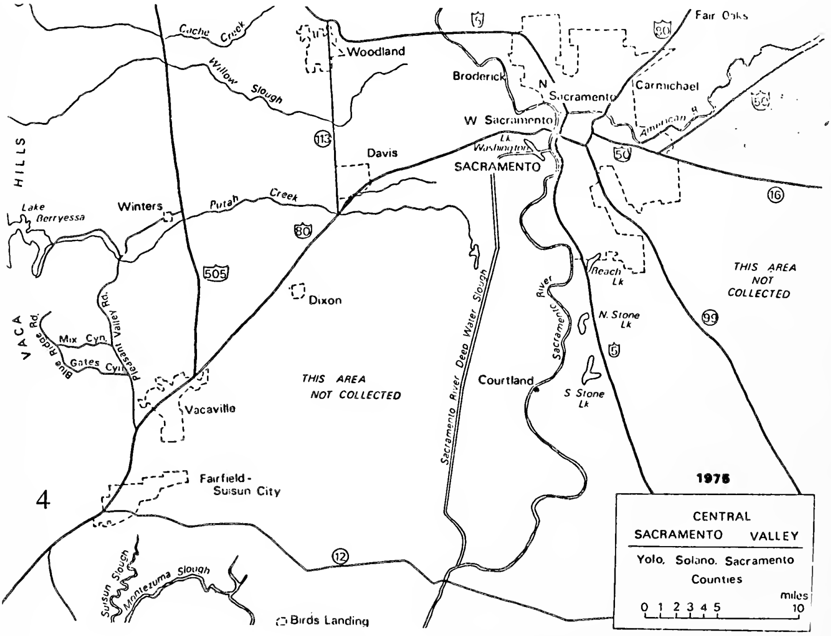
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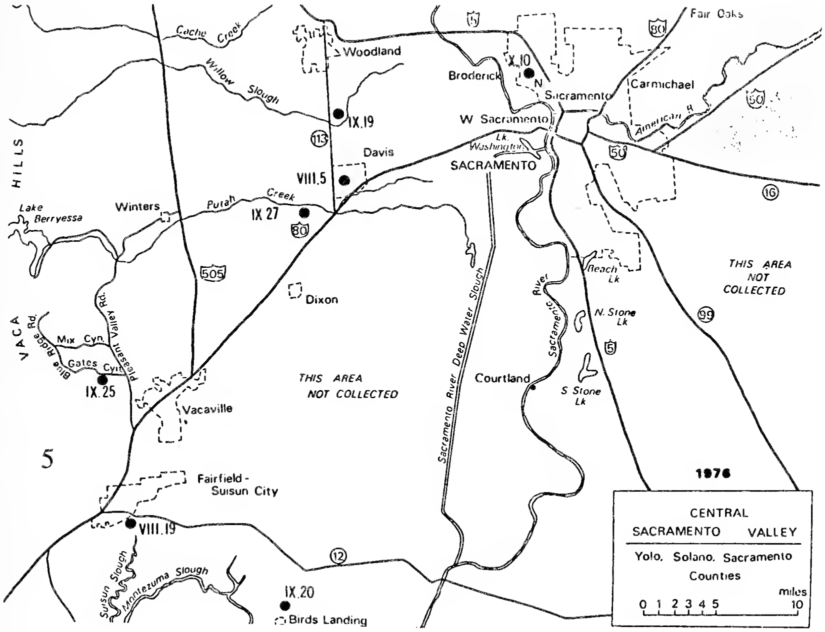
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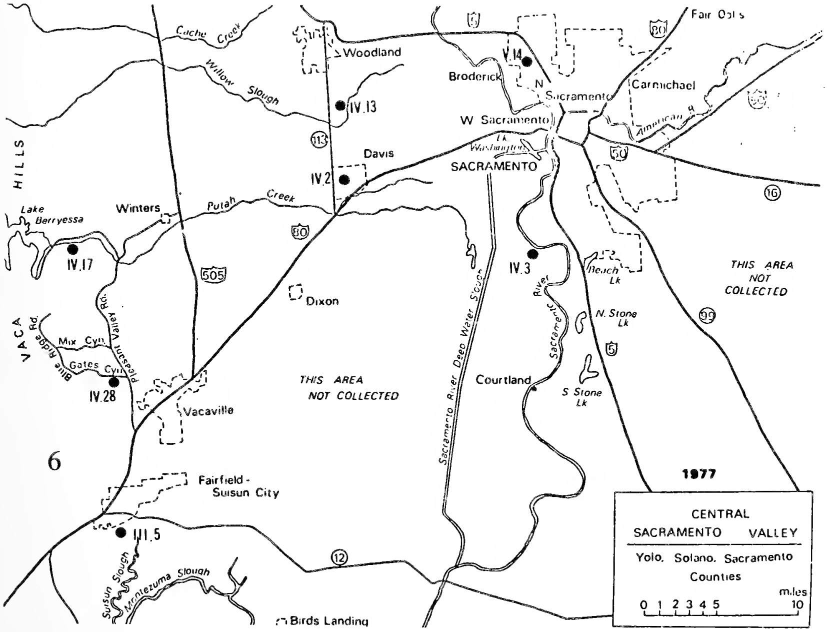
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Montezuma Slough
Birds Landing
1977
CENTRAL SACRAMENTO VALLEY
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ally high population levels, *P. protodice* never reached the Vaca Hills at the western edge of the study area, nor the Fairfield-Suisun area in 1972. However, incredible numbers flew in North Sacramento from late September to late October; in some fields they resembled a snowstorm. The flight there lasted to December 13. Although the first 1972 record at Putah Creek, near Davis, was not until 28 September, large numbers flew there during October and November (last record 22 December).

Autumn 1972 rains were early and excessive, with nearly 200 mm in October and November in locally severe thunderstorms. Severe cold in late November and early December was followed by more cold in late December, and continued heavy rains. Spring 1973 was generally cloudy, cool, and late, with cloudiness holding down daytime temperatures and preventing flight, and keeping night temperatures up, possibly favoring disease. Nonetheless, *P. protodice* overwintered successfully at North Sacramento, where the first brood was common from 18 February - 24 March, and at Putah Creek, 16 January - 15 March. Populations persisted at both places throughout 1973 without reaching 1972 levels. No other peripheral colonies founded in 1972 are known to have persisted into 1973. The overall pattern of late summer colonization resembled 1972, although the western edge of the Valley and the Suisun basin were reached. At the dredge tailings, autumn 1973 population levels were about half those of autumn 1972.

Winter 1973-74 was again very wet. Spring 1974 was mild and sunny; most spring butterflies emerged unusually early. Summer was cool, followed by a long, mild, dry autumn similar to 1971. This season was a disaster for the Checkered White. It was found at only three stations away from the dredge tailings, and populations were poor all season even there. One of the three stations was Putah Creek, where it overwintered so feebly (a second season) that no second generation appeared and the population became extinct; no matings may have taken place. There was no spring brood in North Sacramento, where it was not seen until mid-August.

Winter 1974-75 was wet at first, then turned warm and dry, and ended with a cold, cloudy, wet spring. Cool, moist weather persisted into summer 1975. *Pieris protodice* was apparently completely absent from the study area except on the tailings, where its numbers were even lower than the preceding year — up until autumn. The long, warm autumn of 1975 is generally reckoned to mark the beginning of the California drought. In late September there were very substantial flights on the tailings for the first time since autumn 1973. These continued until mid December, although no outward dispersal was detected. After the mild and extremely dry winter, adults from overwintered pupae began emerging on the tailings on 25 January 1976, only five weeks after the last fall animal was seen. The early spring flight was very large for the season. Populations grew steadily on the tailings, with very high levels almost continuously through 19 November, and the last adult seen 26 December. Strays did not begin showing up off the tailings until August. Early records were at Davis (5 August) and Fairfield-Suisun (19 August), but none was seen at Putah Creek or in the Vaca Hills until the third week of September. The Suisun colonization resulted in a large fall brood, 6-16 October. Based on adult abundance and larval populations in autumn 1976, the pool of overwintering pupae was estimated to be slightly lower than in 1972-73 at the dredge tailings.

Winter 1976-77 was again mild and dry, notable for the number of clear days and the almost total absence of fog. No samples were taken in January or most of February, but on 27 February 1977, *P. protodice* was already abundant on the tailings (sex-ratio, condition, and presence of ova and larvae suggested it had been flying about two weeks). A few days later it was flying at Suisun City, having overwintered there for the first time in this study. By mid-May it was present essentially throughout the range it normally occupies in autumn of a favorable year, and breeding in most of this area. It did not overwinter in 1976-77 at either Putah Creek or North Sacramento, but first brood colonists must have reached Gates Canyon, Willow Slough, and Davis since numbers of fresh animals of both sexes were present there in April, an unprecedented observation. By early summer 1977 *Pieris protodice* was the commonest butterfly throughout the study area and had far surpassed its 1972-73 levels in most places. Snowstorm-like flights occurred near Winters, Woodland, and Dixon, reminiscent of the mass "migrations" of sulphur butterflies in alfalfa fields in the Imperial Valley in the 1940s and 1950s. Disturbed riparian habitats and roadsides supported large breeding populations. It was found abundantly at the head of the Valley at Turtle Bay, Redding, Shasta County, by 26 June; by 15 August it had spread to the 1500 m level in the Trinity Alps northwest of Redding.

At the same time as populations reached extraordinary highs away from the dredge tailings, numbers at the latter began to decline to abnormal lows. By 28 August *P. protodice* was as rare in Rancho Cordova as it had been in 1975. By the third week of August the impact of the two-year drought was conspicuously heavier on the east side of the Valley than elsewhere. Most of the coyote brush (*Baccharis,* Compositae) on the tailings was apparently dead, and both deciduous and live oaks were dropping leaves. The last yellow star thistles (*Centaurea solstitialis* L.) died, removing the principal nectar source. Such adults as could be found on the tailings were clustered around blooming plants of *Senecio Douglassii* DC. (Compositae) on the bank of the American River at Rossmoor Bar.

Following soaking rains between 15-20 September, numbers of butterflies rebounded on the tailings; many Cruciferous seedlings appeared, and some of the seemingly "dead" *Brassica* put on new growth; by 16 October densities were about one-fourth of what they had been on 17 October, 1976.

The Suisun City population also underwent severe strain. There are few *B. geniculata* at Suisun, and most of the large second brood reproduced on *Brassica nigra* (L.) Koch, a winter annual which was in flower at that time. By early summer it was gone, and populations of Whites collapsed in July. *Pieris protodice* managed to persist at a very low level through the second half of the season, and by 14 October numbers were increasing as hosts began to reappear.

HISTORY IN THE SIERRA NEVADA, 1972 - 1977

Phenological samples are also taken routinely along a transect paralleling Interstate 80, from Suisun City at sea level to over 2750 m on Castle Peak, north of Donner Pass. There are sampling stations at 1500 m and 2100 m on the west slope of the Sierra. In 1972 these were located at Marin-Sierra Camp and Boreal Ridge, respectively. In 1973 they were moved to Lang Crossing (South Yuba River) and Donner Pass, where they have remained ever since. *Pieris protodice* has been taken at all the stations along this transect at least as a rare stray, except in the alpine zone on Castle Peak. Comparisons can thus be made between population trends in the Sacramento Valley and in the adjacent mountains. Rainfall and temperature on the west slope by and large vary in tandem with the Valley. This is not true on the east slope, which has a much more continental climate. Relevant weather station data are those for Blue Canyon at about 1500 m and the Central Sierra Snow Laboratory at 2100 m.

Sierran records of the Checkered White are given in Table 2. On the west slope it is rarely taken above the foothills. The mid-elevations are the wettest (Storer and Usinger 1971) and are also heavily forested, with few suitable open, disturbed habitats available. On the east slope *P. protodice* is an overwintering resident to at least 1700 m at the latitude of Highway 80. It is often common at Truckee, and survives the winter there despite very low temperatures. The Checkered White occurs much more commonly at Donner Pass than lower on the west side; this is presumably due to colonization from the east, where it is almost constantly present and has a shorter distance to disperse. Becker's White, *Pieris beckerii* Edwards, which is completely absent from northern and central California west of the Sierra, reaches Donner Pass and breeds some years (Shapiro, 1975b) and is unambiguously of east slope origin. Donner Pass is an "accumulator" of upslope dispersers from both sides (Shapiro, 1973, 1974b). It has not supported overwintering by *P. protodice* during this study.

A sibling species, *P. occidentalis* Reakirt, occurs from 1800 m upward on the west slope at the latitude of Interstate 80. It breeds in subalpine and alpine rocky and disturbed sites (Shapiro, 1976) but does not exclude *P. protodice* competitively below tree line (Shapiro, 1975b). In good years (including 1973, late 1976, and 1977) mixed flights occur at 2100 m. Donner Pass breeding by *P. protodice* may be influenced by Valley conditions, but it is difficult to account for 1975 colonizers when no other west slope records were obtained, and the pool of potential dispersers in the Valley was so low — unless they came from the east. Checkered Whites were at "normal" levels in Truckee and Reno in 1975.

When *P. protodice* occurs at 1500 m on the west slope, it is generally correlated with population levels in the Valley rather than at Donner Pass. On 17 April, 1977, two gravid females of the phenotype eclosing from overwintered pupae were taken ovipositing on *Lepidium* rosettes in a meadow at Lang Crossing.

There had been a large flight at Lang late the preceding summer, and these two animals are best explained not as colonizers but as overwintered individuals. A second brood flew in June, and the population persisted at moderate levels through late October. On April 22, 1977 a male of the *second* brood phenotype, presumably an upslope disperser from the east, was taken in Donner Pass. There was a large flight there, 1 July - 13 October.

Snow packs throughout the northern and central Sierra were at near-record lows in the winter of 1976-77. Warm spring weather began four weeks earlier than average at both 1500 and 2100 m. Normally flights cannot begin for a month after the onset of mild temperatures, because of the heavy snow pack; in 1977 actual flight conditions began in April even at Donner Pass. Normal temperatures and cloudiness in early spring would have prevented successful eclosion at Lang, where *P. protodice* does not normally overwinter.

DENSITY-RELATED FACTORS

Almost nothing is known of predation as a mortality factor on any stage of *P. protodice* in any population. In the Sacramento Valley insect parasitoids are rarely obtained from wild immatures before August. When population densities are very high, the rate of parasitization (by two Tachinids and one Braconid) has not exceeded 10%. The very rapid increases in White populations at Putah Creek in autumn 1972 or on the tailings in autumn 1975 suggest that its reproductive potential can far outstrip the parasitoids, making them important only at times of host scarcity — in a peripheral population, for example, the odds of successful overwintering diminish with every pupa subtracted from the pool by whatever factor.

Shapiro (1970) described density-related emigration from outbreak populations of *Pieris protodice*. When adults are very numerous in a restricted area, constant courting by males forces already-mated females down a gradient of male density, encouraging emigration. Under the extreme drought conditions of late summer 1977, both sexes emigrated from Rancho Cordova; this dispersal may have been density-independent. Many newly emerged Checkered Whites were seen in flower gardens in residential neighborhoods in Sacramento. Although females are often noted in such places during the autumn population peak, it is extremely unusual to find males several kilometers from breeding habitat.

It is now possible to present a crude verbal model of the dynamics of *Pieris protodice* populations in the Sacramento Valley and Sierras.

At low elevations the persistence of a population depends on amount of overwinter survival. This in turn depends on (a) the size of the initial pool of pupae and (b) the winter weather. The pool of pupae is determined by (a) the demography of the population at the time of the last generation of the season and (b) mortality of the last brood of ova and larvae due to density-independent and density-dependent factors.

Large early spring populations, given favorable weather, give rise to rapidly growing late spring ones from which gravid females disperse under density-related pressure, founding new peripheral populations in areas where overwintering rarely occurs. This process may begin as early as the first flight (as in 1977), but is usually conspicuous by September and October.

The dredge tailings on the eastern edge of the Valley offer conditions for reliable overwintering, and thus serve as the ultimate source of colonists to other areas. Large peripheral populations in turn contribute colonists later in the season, founding still more peripheral populations, so that *P. protodice* occupies an increasing proportion of suitable habitats through the season until breeding is interrupted by the onset of winter. Density-independent emigration may occur from any population if host plants and/or nectar sources become unavailable; such emigration involves both sexes.

Colonizing females ascend the west slope of the Sierra Nevada as part of the generalized outflow in all directions from dense Valley populations. They may breed successfully at 1500 m and in very exceptional years, successful overwintering may occur. Colonizers reach Donner Pass (2100 m) more commonly from the east, not necessarily in phase with the dynamics of west slope and Valley populations.

DISCUSSION

How well does this picture correspond to the Ehrlich and

Birch mosaic model? Its general characteristics are very similar: a dynamic system of local populations coming and going stochastically, with a density-related (i.e. deterministic) input into colonization rate. However, extinctions are concentrated at the time of predictable winter stress; and the influence of density operates not through the number of habitats available for colonization — since saturation almost never happens — but the size of the "permanent" dredge tailings populations, which at least in the initial phases are the sole sources of colonizers. Except in 1977, overwintering was virtually confined to them.

The existence of these refuges is not unique to the Sacramento Valley. In the Philadelphia, Pa. - Camden, N.J. area on the Atlantic coast, near the northern boundary of that range, populations of *P. protodice* occur on waste ground, in railroad yards and waterfront areas near the Delaware River. Checkered Whites have bred here at least since the early 1930s, when Orazio Querci studied them; there are anecdotal reports carrying them back before the turn of the century. As in California, peripheral populations appear in vacant lots, along roadsides, and in old fields, extending even onto the Piedmont Plateau northwest of Philadelphia (Shapiro, 1966, 1970), but only one overwintered specimen is on record above the Fall Line although the spring brood occurs reliably near the river. The overall pattern of colonization and extinction is so similar that one suspects the presence of refuges may be a necessary condition for existence near the species border.

The Ehrlich and Birch model probably fits the dynamics of *P. protodice* with even less modification in the Basin-and-Range province and the southern Rockies. It is not known whether the Checkered White reached the Atlantic coast by itself or through human intervention (the type locality, "New York and Connecticut," is at its northeastern limit, where it is virtually confined to sandy beaches). Pacific Coast populations, however, are surely recent. At low elevations west of the Sierran crest there are no native summer Crucifers which could have sustained breeding; *P. protodice* is wholly dependent on weedy species which are thought to have entered California in the Mission Period (Frenkel, 1970). But in the Basin-and-Range province, where overall rainfall is lower, enough rain falls in summer thunderstorms to permit ephemeral blooms of annual (and some perennial) native hosts. In much of the province up-and-downslope colonizations may be essential for survival, but *P. protodice* can

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GYNANDROMORPHS IN HAWAIIAN BUTTERFLIES AND MOTHS

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FROM TIME TO TIME, if also not too often, notes about the occurrence of gynandromorphs in Lepidoptera are published. It may therefore be of interest to lepidopterists to get acquainted with two gynandromorphs which we collected very recently in the field.

One of them is a 1/4 gynandromorph of *Strymon bazochii* Godart, a lycaenid butterfly, the other a 1/2 gynandromorph of *Hedylepta accepta* (Butler), a pyralid moth.

The *Strymon* specimen is as the illustration shows 3/4 ♂ and 1/4 ♀. This appears especially in the characteristic sexual dimorphism of the hindwings (upper and under sides).

The *Hedylepta* specimen is clearly 1/2 ♂ on the left side and 1/2 ♀ on the right side; however, the antennae are ♀ on the left side and ♂ on the right side.

The genitalic dissection of the *Strymon* showed it to be entirely on the male side. There was not the slightest deviation from the normal structure.

The *Hedylepta* had normal female genitalia.

Smith and Perry, 1967, differentiate between gynandromorphs and intersexes, the former being a chromosomal variation, the latter specimens where part of the organism develops toward the opposite sex the chromosomes being normal for the intended sex. Intersexes can be caused by some internal parasites, as infection by *Mermis,* a nematod, or abnormal temperatures.

In the above reported case it will regrettably not be possible to say if we were dealing with real gynandromorphs or intersexes. As, however, nematod infections are often reported in insects in tropical climates it may well be that such infection was the reason for the irregularities in our specimens.

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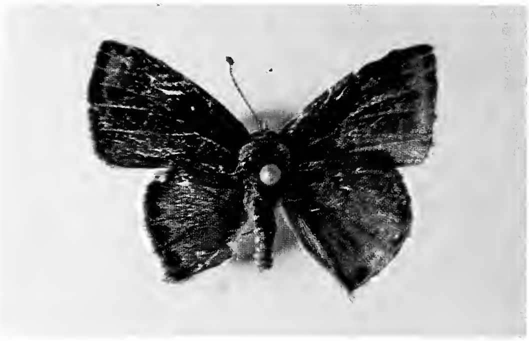

Fig. 1.—*Strymon bazochii* Godart. Hawaii: Oahu, Upper Aina Haina, 13 May 1976, Riotte/Perry.
Fig. 2.—*Strymon bazochii* Godart. Hawaii: Oahu, Upper Aina Haina, 13 May 1976, Riotte/Perry.

Cover Illustration:

Fig. 3.—*Hedylepta accepta* (Butler). Hawaii: Oahu, Waianae Mts., 21 May 1976, A. E. Perry.

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persist indefinitely without refuges. It colonizes in New Mexico above 3000 m.

The dynamic nature of *P. protodice* populations implies that its interaction with *P. occidentalis* is similar to that of the two whirligig beetles (Coleoptera: Gyrinidae) described by Istock (1966). As in that case there is transient competition (Shapiro, 1975b), but one species (*P. occidentalis*) overwinters every year and has a refuge its competitor seems unable to invade (above tree line; however, one female *P. protodice* was collected above 3000 m at Sonora Pass, California, 11 August 1977, *fide* S. Sims). In exceptional years the area of temporary sympatry expands to include much of the Klamath province and the Mount Shasta area.

The vagility and dispersal mechanisms of *P. protodice,* presumably evolved in the Basin-and-Range portion of its present range, preadapt it to colonization and to the conditions now present on the Pacific slope. In the Palaearctic region the ecological equivalent is *Pontia daplidice* Linnaeus (Pieridae), which is a permanent resident in the Mediterranean countries but frequently colonizes far to the north. In 1945 it bred abundantly in parts of southern England (Kettlewell, 1946). In a remarkable paper, Kaisila (1962) documents range changes in 171 species of Fennoscandian Lepidoptera since 1869. He finds that *P. daplidice* was recorded in Finland in 1886, 1892-93, 1896-97, 1909, 1912-13, 1916, 1920, 1922, 1931-36, 1938, 1940, 1942-43, 1946, 1948, 1952, 1957-58 and 1960. It could thus have overwintered about ten times in a century. By and large, occurrences as far north as Finland reflect high population levels to the south and warm, dry weather in central Europe. Kettlewell notes that the 1945 invasion of Britain was preceded by a "quite abnormally hot and early spring."

Species like *P. protodice* and *P. daplidice* are unlikely candidates for speciation in the face of such potentially great gene flow (Ehrlich and Raven, 1969). In this regard they differ greatly from species like *Euphydryas editha,* in which gene flow is so infrequent that even long-term tracking of populations may fail to demonstrate it unless the sampling interval happens to intersect a very abnormal year. The colonizing Pierines would appear to be classic r-species, adapted to ephemeral habitats, surmounting seasonal mortality by high reproductive capacity and colonization. Brussard and Ehrlich (1970) proposed that a widespread availability of host plants would tend to promote such "open" population structures. Their example is *Erebia epipsodea* Butler (Satyridae), a univoltine species whose hosts (grasses) are stable for long periods of time, and which shows few attributes of an r-species. Yet both *E. epipsodea* and *P. protodice* appear to bolster the mosaic model as a valid description of how butterfly populations behave over time. If time scale for population turnover is taken into account, the mosaic model could prove so robust in the face of differing life-styles that it is reduced to a truism.

Every experienced field naturalist acquires notions as to the means by which populations of organisms are regulated. It is much easier to generate them than to document them in a persuasive manner. Uvarov (1931) began a discussion of weather and insect populations which has scarcely run its course to date. The spruce budworm (Morris, 1963) has been amply quantified, but the debate about it still goes on. The critical question is not whether or not we can construct good models of population processes which incorporate causal mechanisms — we can — but whether we judge it worth our while to spend the time and money to collect the most appropriate kinds of data to test them. Such projects are beyond the time scale of Ph.D. dissertation research, and do not give quickly publishable results; but it is essential that they be done. Under the pervasive influence of a theoretical school which is largely vertebrate-oriented, ecologists have acknowledged the primacy of interspecific competition in the organization of communities without demanding documentation. This is an untenable viewpoint if weather is constantly shuffling community composition. Wiens (1977) recently underscored the consequences for ecological theory when we fail to dabble in reality: when predictions are "validated" in the field despite demonstrable invalidity of the theory that generated them, the intellectual structure of the discipline is reduced to a series of intriguing coincidences.

ACKNOWLEDGMENTS

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TABLE 1. Climatological data, Sacramento Executive Airport, California, September 1971 through June 1977; courtesy NWS - NOAA. Because Weather Service measurements are still reported in English units, temperatures below are in degrees Fahrenheit and rainfall is in inches. Headings: (a) Mean high temperature; (b) Mean low temperature; (c) Mean daily temperature; (d) Departure of mean daily T from 30-year mean, 1941-1970; (e) Monthly precipitation; (f) Departure of precipitation from 30-year mean, 1941-1970.

Month and Year		a	b	c	d	e	f
1971	Sept.	88.7	55.6	72.2	+0.7	0.00	—0.19
	Oct.	76.1	46.3	61.2	—2.1	0.13	—0.86
	Nov.	64.7	40.7	52.7	—0.3	0.87	—1.26
	Dec.	50.7	35.2	43.0	—2.8	4.05	+0.93
1972	Jan.	48.5	33.5	41.0	—4.1	0.81	—2.92
	Feb.	61.0	41.8	51.4	+1.6	1.28	—1.40
	Mar.	71.6	45.5	58.6	+5.6	0.29	—1.88
	Apr.	71.7	45.4	58.6	+0.3	1.39	—0.15
	May	83.6	50.1	66.9	+2.6	0.28	—0.23
	June	90.3	54.6	72.5	+2.0	0.19	+0.09
					Water year total:		9.29”
	July	93.5	58.5	76.0	+0.8	0.00	+0.01
	Aug.	93.2	58.5	75.9	+1.8	0.00	—0.05
	Sept.	84.3	54.6	69.5	—2.0	0.90	+0.71
	Oct.	72.5	51.5	62.0	—1.3	1.75	+0.76
	Nov.	56.5	42.8	49.7	—3.3	5.14	+3.01
	Dec.	46.8	34.3	40.6	—5.2	1.88	—1.24
1973	Jan.	51.6	37.0	44.3	—0.8	6.87	+3.14
	Feb.	60.3	45.9	53.1	+3.3	5.64	+2.96
	Mar.	60.0	42.2	51.1	—1.9	2.76	+0.59
	Apr.	74.8	46.7	60.8	+2.5	0.05	—1.49
	May	85.1	53.6	69.4	+5.1	0.13	—0.18
	June	91.4	57.7	74.6	+4.1	0.00	—0.10
					Water year total:		25.12”
	July	94.9	58.7	76.8	+1.6	0.00	—0.01

	Aug.	91.7	56.7	74.2	+0.1	0.00	—0.05
	Sept.	86.3	55.3	70.8	—0.7	0.33	+0.14
	Oct.	77.1	49.7	63.4	+0.1	1.64	+0.65
	Nov.	59.3	44.4	51.9	—1.1	6.27	+4.14
	Dec.	52.5	41.2	46.9	+1.1	2.79	—0.33
1974	Jan.	53.2	39.3	46.3	+1.2	3.58	—0.15
	Feb.	58.7	38.1	48.4	—1.4	1.37	—1.31
	Mar.	62.9	45.2	54.1	+1.1	3.27	+1.10
	Apr.	68.5	44.6	56.6	—1.7	0.96	—0.58
	May	80.1	47.5	63.8	—0.5	0.01	—0.50
	June	86.8	54.1	70.5	0.0	0.50	+0.40
					Water year total:		20.72"
1975	Jan.	50.9	35.9	43.4	—1.7	0.73	—3.00
	Feb.	57.3	41.0	49.2	—0.6	4.59	+1.91
	Mar.	58.5	42.1	50.3	—2.7	4.28	+2.11
	Apr.	63.2	40.3	51.8	—6.5	0.81	—0.73
	May	83.9	52.4	68.2	+3.9	T.	—0.51
	June	89.8	56.6	73.2	+2.7	T.	—0.10
					Water year total:		15.88"
	July	94.0	60.5	77.3	+2.1	0.04	+0.04
	Aug.	93.2	60.6	76.9	+2.8	0.23	+0.18
	Sept.	94.0	60.7	77.4	+5.9	T.	—0.19
	Oct.	77.4	52.7	65.1	+1.8	2.03	+1.04
	Nov.	65.1	44.0	54.6	+1.6	0.29	—1.84
	Dec.	56.9	37.8	47.4	+1.6	0.18	—2.94
1976	Jan.	59.5	34.8	47.2	+2.1	0.36	—3.37
	Feb.	62.0	41.7	51.9	+2.1	1.49	—1.19
	Mar.	67.4	41.8	54.6	+1.6	0.44	—1.73
	Apr.	70.6	45.2	57.9	—0.4	1.53	—0.01
	May	86.7	53.4	70.1	+5.8	0.00	—0.51
	June	90.0	57.7	73.9	+3.4	0.04	—0.06
					Water year total:		6.63"
	July	93.4	59.5	76.5	+1.3	0.00	—0.01
	Aug.	87.6	59.2	73.4	—0.7	0.65	+0.60
	Sept.	86.3	57.3	71.8	+0.3	0.52	+0.33
	Oct.	81.1	51.0	66.1	+2.8	0.02	—0.97
	Nov.	66.7	46.6	56.7	+3.7	0.55	—1.58
	Dec.	59.5	33.5	46.5	+0.7	0.65	—2.47
1977	Jan.	50.3	37.3	43.8	—1.3	1.17	—2.56
	Feb.	64.0	40.8	52.4	+2.6	1.17	—1.51
	Mar.	62.7	39.3	51.0	—2.0	1.27	—0.90
	Apr.	77.2	47.1	62.2	+3.9	0.30	—1.24
	May	71.4	47.3	59.4	—4.9	0.73	+0.22
	June	88.1	56.2	72.2	+1.7	0.00	—0.10
					Water year total:		7.03"

TABLE 2. Records of *P. protodice* at Sierran sampling stations, 1972-1977. For locations of stations, see text.

Year	1500 m	2100 m
1972	x.4	ix.7
1973	none	vi.27-ix.28, breeding
1974	ix.25	none
1975	none	ix.13 - ix.25
1976	viii.23 (common)	viii.13-20 and x.4 - xi.20, breeding
1977	iv.17 (over-wintered) vi.15-x.20,breeding	iv.22 (immigrant) and vii.1-x.13, breeding

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THE NOMENCLATURE IN AN IMPORTANT BRITISH CHECK LIST (1972)

PART 4: CORRECT GENDER FOR SOME OTHER GENERIC NAMES

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THE FOREGOING PART 3 (*J. Res. Lep.* 13:179-180) was written to correct improper usage of gender for many generic names derived from the Classical without change of termination. The present Part 4, on the other hand, records errors in gender for those genus-group names (GGN) which either changed their original Greek termination or are products of a different formation mode.

GGN formed from modern personal names

Ochsenheimeria (fem.) *mediopectinella* (not *mediopectinellus*).

Crombrugghia (fem.) *laeta* (not '*laetus*').

GGN ending in a definite Greek (or Latin) suffix

Calybites (masc.) *pyrenaeellus* (not '*pyrenaeella*'), *C. phasianipennellus* (not -ella), and *C. auroguttellus* (not -ella).

Teleiodes (masc.) with 10 species listed nine of which are treated as if *Teleiodes* were of feminine gender.

Chionodes (masc.) *fumatellus* (not '*fumatella*') and *C. distinctellus* (not -ella).

Epichoristodes (masc.) *acerbellus* (not '*acerbella*').

Philedonides (masc.) *lunanus* (not '*lunana*').

Tortricodes (masc.) *alternellus* (not '*alternella*').

Stenodes (masc.) *alternanus* (not '*alternana*') and *S. stramineus* (not -ea).

Peribatodes (masc.) *rhomboidarius* (not '*rhomboidaria*').

Cleorodes (masc.) *lichenarius* (not '*lichenaria*').

Psodos coracinus (not '*coracina*'). Lapsus for *Psolos* (masc.).

Aspitates gilvarius (not *'gilvaria'*) and *A. ochrearius* (not *'ochrearia'*). Lapsus for *Aspilates* (masc.).

Heliothis. According to the investigation done by Steyskal, (1971), the gender of this Latinized name is clearly masculine. A statement which confirms the correct usage of *Heliothis* by Staudinger and Wocke (1871, who treated it explicitly as masculine noun one hundred years before Steyskal. Thus, the necessary agreement in gender requires to correct names of three species and one subspecies listed: *Heliothis maritimus* (not *'maritima'*), *H.m.bulgaricus* (not *'maritima bulgarica'*), *H.nubiger* (not *'nubigera'*), and *H.peltiger* (not *'peltigera'*). Moreover, the subfamily based on *Heliothis* (genitive Heliothis) is to be named *Heliothinae*, instead of the currently used *Heliothidinae* (see Hardwick, 1970). This means that while *Chromonema heliothidis* is the specific name of a recently described Nematod parasite of *Heliothis zea* does not comply with the rules of correct formation; the name of *Baculovirus heliothis*, an organism used for control of *Heliothis* larvae on cotton, etc., is formed in harmony with the etymology and grammar.

Grammodes (masc.) *stolidus* (not *'stolida'*).

GGN derived from Greek with a change of termination

Hepialus (masc.) *sylvinus* (not *'sylvina'*) and *H.fusconebulosus* (not -osa).

Ateliotum (neuter) *insulare* (not *'insularis'*).

Caryocolum (neuter) with *C. vicinellum* (not *'vicinella'*), *C. alsinellum* (not -ella), *C. viscariellum* (not ella), *C. marmoreum, C. fraternellum* (not *'fraternella'*), *C. proximum, C. blandellum* (not *'blandella'*), *C. junctellum* (not -ella), *C. tricolorellum* (not -ella), *C. blandulellum* (not -ella), *C. huebneri*, and *C. knaggsiellum* (not *'knaggsiella'*) included.

Euchromius (masc.) *ocelleus* (not *'ocellea'*).

Crambus (masc.) with *C. pascuellus* (not *'pascuella'*), *C. leucoschalis, C. silvellus* (not *'silvella'*), *C. uliginosellus, C. ericellus* (not *'ericella'*), *C. hamellus* (not -ella), *C. pratellus* (not -ella), *C. nemorellus* (not -ella), and *C. perlellus* (not -ella) included.

Chrysocrambus (masc.) *linetellus* (not *'linetella'*) and *C. craterellus* (not -ella).

Schoenobius (masc.) *gigantellus* (not *'gigantella'*) and *S. forficellus* (not -ella).

Cnaemidophorus (masc.) *rhododactylus* (not '*rhododactyla*').

Platyptilia (fem.) *isodactyla* (not '*isodactylus*').

Stenoptilia (fem.) *zophodactyla* (not '*zophodactylus*').

Pterophorus (masc.) *tridactylus* (not '*tridactyla*'), *P. pentadactylus* (not '*pentadactyla*'), and *P. galactodactylus* (not '*galactodactyla*').

Pselnophorus (masc.) *heterodactylus* (not '*heterodactyla*').

Leioptilus (masc.) *carphodactylus* (not '*carphodactyla*') and *L. tephradactylus* (not '*tephradactyla*').

Oidaematophorus (masc.) *lithodactylus* (not '*lithodactyla*').

Bupalus (masc.) *piniarius* (not '*piniaria*'). Derivation of the specific epithet: pinus — piniarius, like arena — arenarius.

Agrius (masc.) *cingulatus* (not '*cingulata*').

Smerinthus (masc., although derived from a Greek feminine noun, viz. smerinthos = merinthos) *ocellatus* (not '*ocellata*').

Heliophobus (masc.) *reticulatus* (not '*reticulata*'), ssp. *marginosus* (not '*marginosa*') and ssp. *hibernicus* (not '*hibernica*').

Tathorhynchus (masc., although derived from a Greek neuter noun, viz. rhynchos) *exsiccatus* (not '*exsiccata*').

ACKNOWLEDGEMENT

The author is indebted to Dr. George C. Steyskal, Research Entomologist of the Systematic Entomology Laboratory, USDA, Washington, D.C. for reading critically the manuscript. A full agreement has been reached on the gender of all genus-group names referred to.

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BIOCHEMICAL STUDIES OF THE LARVAL HOSTS OF TWO SPECIES OF *LYCAENA* FABRICIUS[1]

(LYCAENIDAE)

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INTRODUCTION

ALTHOUGH THE HOPKINS HOST SELECTION PRINCIPLE (Hopkins 1916, 1917) relating larval host plant specificity and speciation in insects has been discredited (Wood, 1963; Mayr, 1969), many lepidopterists persist in citing larval host preference (plant species) as a basis for separating butterfly species. In the course of a study of the lycaenid butterfly complex *Lycaena dorcas* Kirby and *L. helloides* (Boisduval), I examined some of the biochemical properties of their larval hosts. East of the Rocky Mountains, the two species are allopatric and phenotypically separable. Larvae of *L. helloides* use the Polygonaceae (*Polygonum, Rumex*) while *L. dorcas* appears restricted to *Potentilla* (Rosaceae). *L. dorcas* is univoltine while *helloides* is multivoltine. From the Front Range of the Rockies westward to California and north to Alaska, numerous *dorcas/helloides* phenotypes occur which reflect altitudinal and latitudinal gradients. The published host plant studies (Chambers, 1963; Shapiro, 1974) indicate oviposition on either *Potentilla* or the Polygonaceae under laboratory conditions. In the field, distinct preferences are apparent. To gather information for a taxonomic revision of this butterfly group (to be published separately), samples of *Rumex, Polygonum* and *Potentilla* were subjected to various analyses with the results reported below.

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METHODS AND RESULTS

Botanically the Polygonaceae and Rosaceae are rather disparate families. Ehrlich and Raven (1964), and Dethier (1952) have discussed olfactory adaptation and some of the chemical attractants involved in insect selection of oviposition substrate. The flavonoids are one of the classes of compounds cited. Accordingly, plant specimens were examined for biochemical commonalities and the presence of flavonoids. Specimens of *Polygonum amphibium* L., a known host of *L. helloides* in McHenry Co., Illinois, were obtained from that locality. *Potentilla fruticosa* L., a known host for *L. dorcas,* and *Rumex triangulivalvis* (Danser) Rechinger, a suspected host for *L. helloides* in eastern Wyoming (females in association with the plants) were obtained from the Sherman Range, Laramie Mountains, Albany Co., Wyoming.

Extracts were prepared by soaking the leaves over night in 95% ethanol. Equal weights of leaf material were suspended in equal volumes of alcohol, although no quantitative measurements were attempted. The extracts were then scanned over the range 200-750 nm using a Beckman 25 double-beam scanning spectrophotometer with the extracting alcohol as a blank. The spectral signatures for the three samples are shown in Figure 1. Except for concentration levels, they are nearly identical. The absorption at ca. 670 nm is chlorophyll; the weak absorption at ca. 550 nm and the broad absorption centered about 350-370 nm are unclear. The seemingly weak absorption lines at 250-260 nm (note that there has been a 20:1 vertical scale change in the traces) represent flavonoid compounds, as subsequently confirmed; the very strong absorption at ca. 210 nm is characteristic of organic oxygen compounds.

To confirm the presence of flavonoids, two-dimensional descending paper chromatography studies were conducted using Whatman no. 1 chromatography paper. 46 x 57 cm sheets were used with the alcohol extract sample spotted in one corner. Solvent 1 indicated as the vertical axis in Figure 2 was by volume 3 parts tertiary butyl alcohol, 1 part glacial acetic acid, 1 part distilled water. The 57 cm paper length was used for this 24 hour run. For the 4-5 hour horizontal axis run, 15% glacial acetic acid was used. The R values were determined, by reading the dry chromatogram over ultraviolet light, and plotted (Fig. 2).

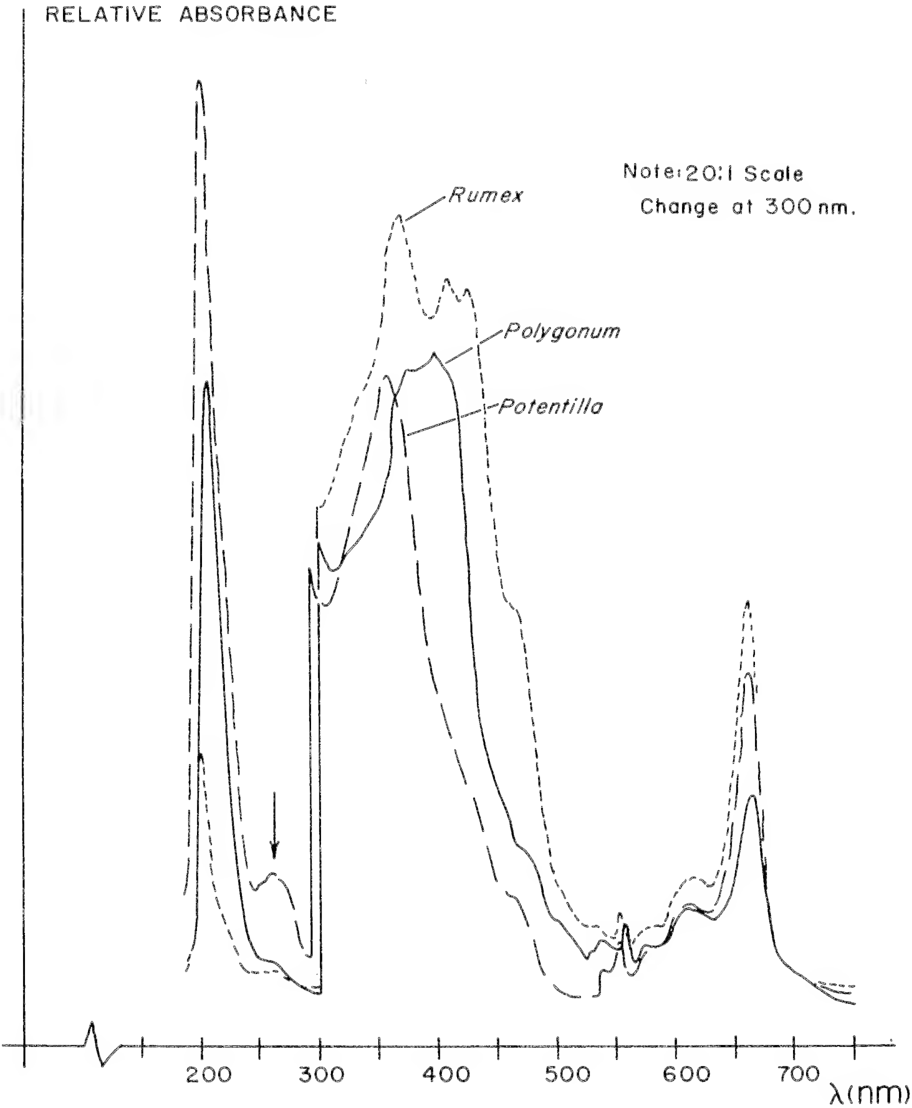

Fig. 1 — Spectral signatures of the three plant species studied. The arrow points to flavonoid absorption.

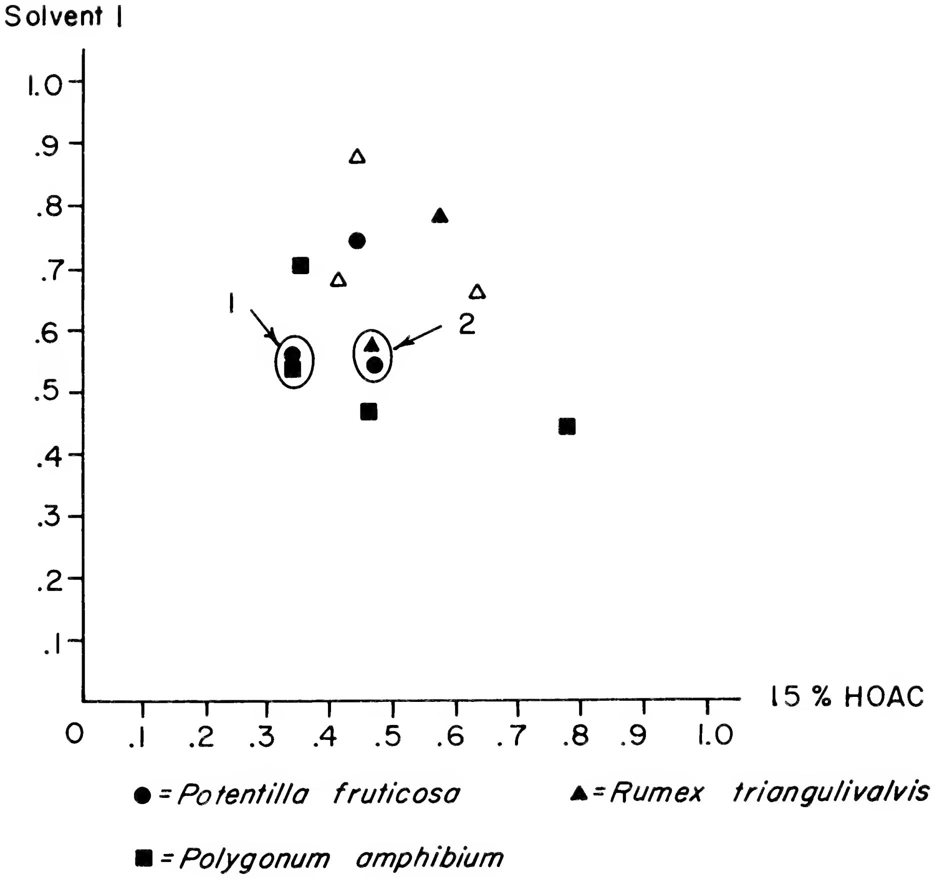

Fig. 2. — Two-dimensional chromatogram of the compounds present in the three plant species studied. The axis coordinates are the R values. The open triangles represent non-flavonoid compounds.

The solid symbols represent flavonoid compounds, probably flavones ($C_{15}H_{10}O_2$) which appear as "dust" on leaves and stems. As a further check, the spots indicated by "1" in the figure were eluted with methanol and scanned spectrophotometrically. Both exhibited strong absorption at ca. 252 nm, characteristic of flavonoids, and both absorbed strongly at 210 nm, characteristic of organic oxygen compounds. No other spectral lines were detected over the range 200-750 nm.

Steam distillations of freshly collected samples of the *Potentilla* and *Rumex* were conducted to recover any volatile oils. This was not done for the Illinois *Polygonum* specimens, as they were of insufficient volume and had dried out. The very small amounts of residue obtained were dissolved in chloroform and spectrophotometrically scanned. Both exhibited strong absorption lines at ca. 250 nm, characteristic of a benzene ring aromatic, probably a flavonoid. Both curves also exhibited a "knee" at ca. 260 nm, indicating that probably two compounds with slightly separated absorption lines were present. Chromatographic cross checking was not possible because of the very low concentrations of the samples.

CONCLUSIONS

Biochemically, *Rumex, Polygonum* and *Potentilla,* used as larval hosts by *L. dorcas* and *L. helloides,* are very similar. *Potentilla fruticosa* and *Polygonum amphibium* appear to contain a common, or very closely related, flavonoid compound as shown in Figure 2. Within the accuracy of paper chromatography, *P. fruticosa* and *R. triangulivalvis* may also contain a common flavonoid as indicated by "2" (Fig. 2). The volatile oils study indicates that *R. triangulivalvis* and *P. fruticosa* are very similar. Based upon the spectral signatures (Fig. 1), one would expect that *P. amphibium* also has a similar volatile component, since all three plants exhibit absorption lines characteristic of benzene ring aromatics.

If females of *L. dorcas* and *helloides* depend upon olfactory stimuli in host plant perference, then it would seem that either *Potentilla* or *Polygonum/Rumex* could be selected as oviposition substrates. This has been demonstrated under laboratory conditions as noted above. Based upon this study, it would appear that in some cases the basis for selection of oviposition substrate and larval host in the monophagous and oligophagous Lepidoptera is biochemical similarity of plants and not their taxonomic placement. Depending upon environmental conditions and olfactory adaptation in a given butterfly colony, a particular host is preferred, but rather disparate plant species may be quite similar biochemically and thus found suitable.

ACKNOWLEDGEMENTS

I would like to thank Dr. A. Duane Anderson, School of Pharmacy, Dr. R. Owen Asplund, Department of Chemistry and Biochemistry, and Dr. Daniel J. Crawford, Department of Botany, University of Wyoming for providing access to their laboratory equipment and assistance in interpretation of the experimental results. Mr. Irwin Leeuw of Cary, Illinois kindly provided the *Polygonum* plants.

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BUTTERFLIES OF THE HAWAIIAN ISLANDS

ACCORDING TO THE STAND OF LATE 1976

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Different reasons could be quoted for this informative paper: first the fact that in some recently published compendia, like Lewis, *Butterflies of the World* (1973) and Howe, *The Butterflies of North America* (1975), some of the butterflies of the Hawaiian Islands which, as everybody knows, belong to the Indo-Australian fauna, are entirely or partially included with the bulk of the nearctic species; second the fact that the interest in our lepidopterous fauna is growing as we see from Ehrlich's paper (1976) and the many letters and phone calls from interested collectors visiting the Islands. Here then shall be a short annotated list of what we have at the moment, when it was first recorded and from where it reached us, if known.

HESPERIIDAE

1. *Erionota thrax* (Linné), the banana skipper, a native of most of S and E Asia, including India, China, Moluccas, Malaya, Philippines, Guam. First recorded in August 1973 at Hickam Air Force Base, Honolulu. During 1974 established also on Kauai and Maui, throughout 1975 on Hawaii, Molokai and Lanai. Regrettably the damage this large and beautiful skipper is able to inflict on banana plantations can be extensive.

2. *Hylephila phyleus* (Drury), the fiery skipper, a native of South and North America and the West Indies. First recorded 8 September 1970 at Salt Lake, Honolulu, a short distance north of Honolulu International Airport and Hickam Air Force Base. Until 1974 only on Oahu, in October 1974 also on Hawaii. Not damaging to lawns as it is usually on the mainland.

PAPILIONIDAE

3. *Papilio xuthus* Linné, the citrus swallowtail, with a wide range from India through China to Korea, Japan, Formosa, Ryukyu and Bonin Islands, Philippines, also Siberia, Burma, Guam. First recorded during April 1971 at Salt Lake, Honolulu; June 1972 in Kauai; June 1974 in Maui and Hawaii; August 1974 in Molokai and September 1974 in Lanai.

PIERIDAE

4. *Pieris rapae* (Linné), the cabbage butterfly, almost cosmopolitan. According to Perkins (1913) appeared first, introduced with cabbages from California, in 1897. There is no seasonal dimorphism in the Hawaiian cabbage butterflies. All specimens belong to the European summer form. The species is, of course, found on all islands.

DANAIDAE

5. *Danaus plexippus* Linné, the monarch butterfly. Perkins (1913) says: "no doubt a natural immigrant, which has established itself in the islands since the introduction of the milkweed, on which it feeds, by foreigners," between 1845 and 1850. Albino monarch butterflies occur not infrequently.

HELICONIIDAE

6. *Agraulis vanillae* (Linné), the "gulf fritillary". For the first time taken in Honolulu, Manoa, 14 January 1977 by Keith T. Arakaki and Elizabeth A. Perry, both of the Department of Entomology, B. P. Bishop Museum. There were many males and females of the species on the wing and it seems to be well established although there is not the slightest suggestion how it may have arrived on the island.

NYMPHALIDAE

7. *Vanessa (V.) atalanta* (Linné), the red admiral. First found on Hawaii by Perkins. Probably introduction after Blackburn's time (1876-1882) because Blackburn did not find it. Restricted to the island of Hawaii, except for a single worn specimen collected by Swezey on 27 June 1932 at Kumawela, Kauai, and preserved in the collection of the State Dept. of Agric., Honolulu.

8. *Vanessa (V.) tameamea* Eschscholtz, the Kamehameha butterfly. Endemic. Throughout the forests of all islands. Collected by J. F. Eschscholtz, surgeon-naturalist of the Russian Cpt.

Kotzebue South Seas and Bering Straits expedition 1815-1818, and described by him 1821. Zimmerman (1958) considers it to be a derivative of *Vanessa indica* (Herbst), a great wanderer—as he says—which is known from Madeira, the Canary and Balearic Islands, Portugal and southern Spain, and is widespread over the Indo-australian faunal region, even into the Marianas and vicinity. However, one has also to give some thought to the possibility, suggested by other authors, of an immigration from New Zealand, where *Vanessa (V.) gonerilla* (Fabricius) is endemic, via the Line Islands. The latter species is also nearly related to *V. (V.) indica.*

9. *Vanessa (Cynthia) cardui* (Linné), the painted lady. Cosmopolitan. Perkins (1913) considers it and the following as natural immigrants. Already found by Blackburn. On all islands.

10. *Vanessa (Cynthia) virginiensis* (Drury), Hunter's butterfly or the American painted lady. North America, Canary Islands, South America to Brazil. Already found by Blackburn. On all islands.

LYCAENIDAE

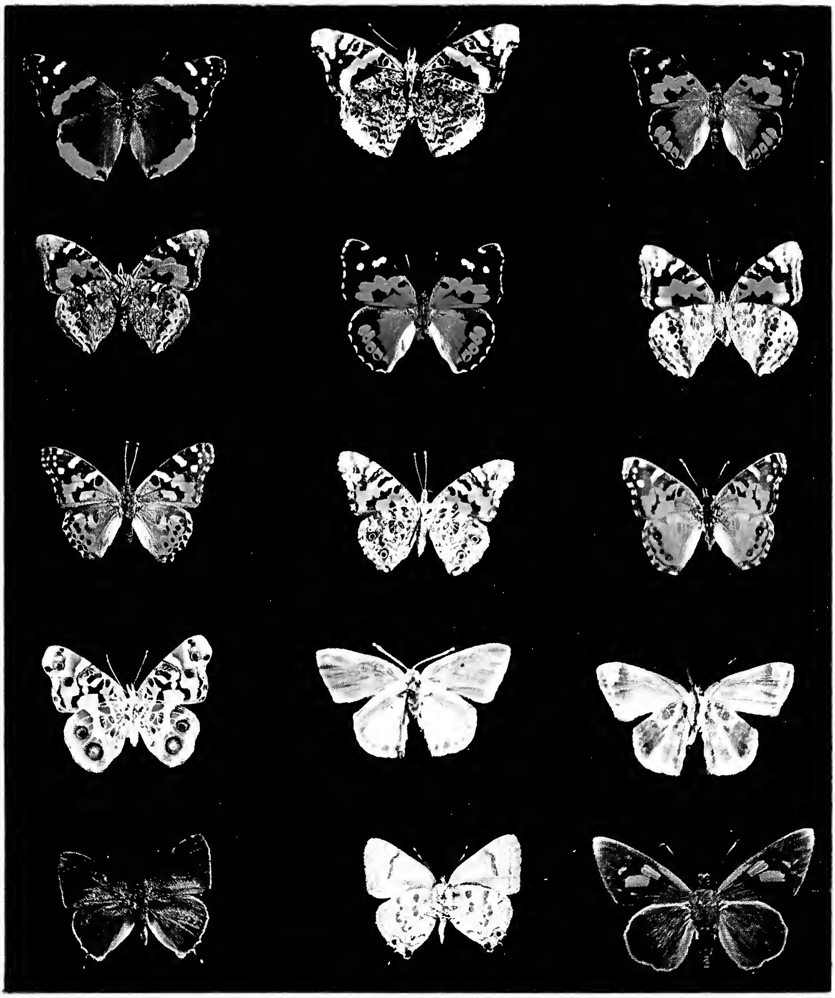
11. *Strymon bazochii* Godart, the smaller lantana butterfly. Purposely introduced from Mexico 1902 by Koebele to aid in the control of *Lantana*. On all islands. The population belongs to nominate *bazochii* not to the "subspecies" *gundlachianus* (Bates) —H. K. Clench *in litt.*

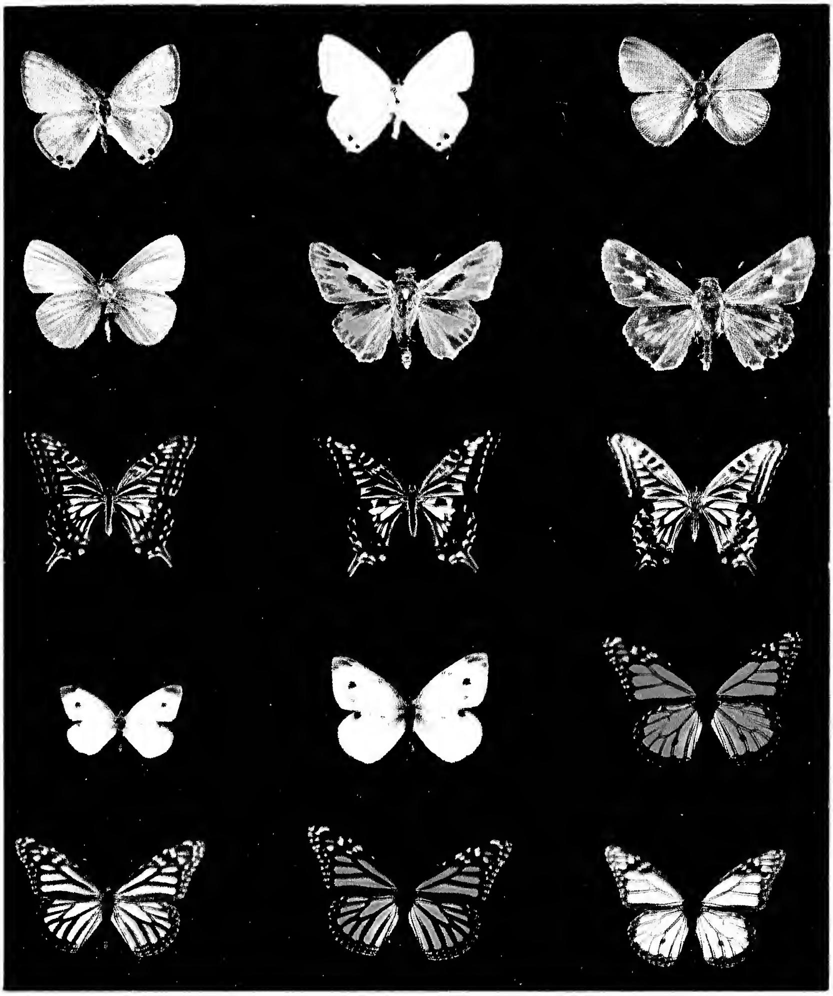
12. *Thmolus echion* (Linné), the larger lantana butterfly. Same as before. On all islands. At least on Oahu getting recently somewhat rare.

13. *Lampides boeticus* (Linné), the bean butterfly. Widespread from Africa, southern Europe to India and the Orient to Malaya and Australia. First taken by Blackburn before 1882. A very common butterfly on all islands.

14. *Vaga blackburni* (Tuely), Blackburn's blue. Endemic. On all islands. Not rare. Principal host plant *Acacia koa.* Zimmerman (1958) hypothesizes its origin from the Bonin Islands where the only known near relative, *V. ogasawaraensis* (Pryer) lives.

15. *Brephidium exilis* (Boisduval). Western pigmy blue. For the first time caught at the end of June 1978 at Hickam Airforce Base, Honolulu, and then again at the beginning of August by L. Nakahara *et al.*, Hawaii State Dept. of Agric. It is endemic





in southern Texas, strays north to Nebraska, ranges west to the Pacific, south to Venezuela. It has all the potentialities to become common.

From this list it can be easily understood that in our days all facts speak for the immigration of insects new to the Islands of Hawaii by airplane, from both sides, west and east, however, mostly from the west. There it is possible to trace many of them to Okinawa and Guam. This is still more underlined when we add to the butterflies our most recent newcomers among the Sphingidae:

Theretra nessus (Drury), first specimen taken at a light 14 August 1974 at Campbell Industrial Park at Barbers Point, west of Pearl Harbor. Known in Okinawa.

Deilephila nerii (Linné), first specimen taken at Hickam Air Force Base, 18 September 1974. Known in Okinawa.

Macroglossum pyrrhostictum (Butler), in a house at Makiki, a Honolulu suburb, 11 July 1976. Known in Okinawa.

In the case of *D. nerii* the transport vehicle seems very well pointed at, in the other two cases at least the possibility according to presently available knowledge of distribution is given.

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For continued information about Hawaiian insects, recent introductions, spreading of previously reported ones and related questions, use: State of Hawaii, State Department of Agriculture a.o., *Hawaii cooperative economic insect report.* This is a weekly publication which was begun in 1966.

PLATE 1: Read left to right and down. 1. *Vanessa atalanta* (Linne), Olaa, Oahu, dorsal view; 2. same, ventral view; 3. ♂ *V. tameamea* Esch., Kilauea, Oahu, dorsal view; 4. same, ventral view; 5. ♀ *V. tameamea* Esch., Kilauea, Oahu, dorsal view; 6. same, ventral view; 7. *V. cardui* (Linne), Pearl City, Oahu, dorsal view; 8. same, ventral view; 9. *V. virginiensis* (Drury), Leilehua, Oahu, dorsal view; 10. same, ventral view; 11. *Strymon bazochii* Godart, Honolulu, Oahu, dorsal view; 12. same, ventral view; 13. *Thmolus echion* (Linne), Palolo, Oahu, dorsal view; 14. same, ventral view; 15. ♂ *Erionata thrax* (Linne), Honolulu, Oahu, dorsal view.

PLATE 2: Read left to right and down. 1. ♂ *Lampides boeticus* (Linne), Mapulehu, Molokai, dorsal view; 2. same, ventral view; 3. ♂ *Vaga blackburni* (Tuely), Pauoa, Oahu, dorsal view; 4. same, ventral view; 5. ♂ *Hylephila phyleus* (Drury), Salt Lake, Oahu, dorsal view; 6. ♀ *H. phyleus* (Drury), Salt Lake, Oahu, dorsal view; 7. ♂ *Papilio xuthus* Linne, Kaimuki, Oahu, dorsal view; 8. ♀ *P. xuthus* Linne, Kaimuki, Oahu, dorsal view; 9. same, ventral view; 10. ♂ *Pieris rapae* (Linne), Nuuanu, Oahu, dorsal view; 11. ♀ *P. rapae* (Linne), Waikane, Oahu, dorsal view; 12. ♂ *Danaus plexippus* (Linne), Manoa, Oahu, dorsal view; 13. ♀ *D. plexippus* (Linne), Nuuanu, Oahu, dorsal view; 14. ♀ *D. plexippus* (Linne), Honolulu, Oahu, dorsal view; 15. ♀ *D. plexippus* (Linne), Waimanalo, Oahu, dorsal view.

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THE IDENTITY OF THE ROCKY MOUNTAIN *LYCAENA DORCAS-HELLOIDES* COMPLEX (LYCAENIDAE)

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ABSTRACT

High altitude Rocky Mountain *Lycaena* of the *dorcas* Kirby and *helloides* (Bdv.) group have been variously assigned to *dorcas* or *helloides* by different authors. I have attempted to show that all Rocky Mountain material is actually *L. helloides*, both at low and high altitude. Natural larval foodplants for the high-altitude populations were previously unknown; five Polygonaceae plant species are reported from observations in nature. *L. dorcas*, in contrast, is known to feed on *Potentilla* (Rosaceae); *L. helloides* from other regions also feeds on Polygonaceae. Lastly, my data indicate that high altitude material is closest to *helloides* in six of eight wing pattern and wing shape characters, two of the characters being variable.

INTRODUCTION

High-altitude Rocky Mountain *Lycaena* of the *dorcas* and *helloides* group have recently been assigned to *L. helloides* (P. Opler, in Howe 1975), and to *L. dorcas* (Ferris 1977). Earlier authors were uncertain as well. Clench (1961) emphasized the need for careful field studies in the Rocky Mountains, a need which has not been met. I therefore decided to try to clarify the identity of Rocky Mountain populations using foodplant studies and detailed studies of morphology. I found that there are no differences in male or female genitalia between *dorcas* and *helloides*. My studies indicate that high-altitude Rocky Mountain material belongs to *helloides*. Both the larval foodplants and the details of wing pattern and wing shape indicate that high-altitude Rocky Mountain material is closest to *helloides*. High altitude Rocky Mountain populations seem to be rather general feeders on *Rumex* and *Polygonum* (both Polygonaceae), as are populations of *helloides* in most of its range in North America.

My study also indicates a large amount of individual and altitudinal variation in several wing pattern characteristics, which may indicate environmental influences on phenotype and may bring into question some subspecies that have been proposed in the *dorcas-helloides* group; geographic variation seems to involve a combination of genetic and environmental changes which are difficult to unravel.

I use *Lycaena* as the genus name rather than *Epidemia* as does Ferris (1977) because *Lycaena* is a time-honored genus and I think that relationships within the Lycaenidae are better served by treating *Epidemia* and other names as subgenera.

FOODPLANTS — GENERAL

L. dorcas apparently uses mostly *Potentilla fruticosa* (Rosaceae) as its larval foodplant. Larval foodplant records are known for Michigan (*P. fruticosa,* Newcomb 1911), Ohio (*P. fruticosa,* Price 1970), Ontario (*P. fruticosa,* P. M. Catling, W. Edmonds, C. H. Walker 1970 unpublished manuscript), Maine (*P. fruticosa,* Brower 1974, for *L. dorcas claytoni* (Brower)), New Brunswick (*Potentilla,* Klots 1951, for *L. dorcas dospassosi* (McDunnough); Shapiro 1974b states that this supposedly *dorcas* population probably feeds on *Potentilla egedei* var. *groenlandica* or *P. anserina*).

L. helloides, in contrast, feeds almost exclusively on Polygonaceae: *Polygonum aviculare, P. lapathifolium, P. hydropiperoides* (all southern California, Coolidge 1924), *P. aviculare, P. lapathifolium, P. persicaria, P. punctatum* (all central California, Shapiro 1974a), *P. amphibium* (Tietz 1972), *Polygonum* probably *careyi* (Michigan, Clench 1950), *Rumex* sp. (Washington, Robert Pyle, Lepid. News 1976 #2), *R. persicarioides, R. conglomeratus, R. crispus, R. hymenosepalus* (all southern California, Coolidge, 1924), *R. crispus* (central Calif., Shapiro 1974a), *R. acetosella* (Garth & Tilden 1963). A record of *Oxytheca spergulina* (Lembert 1894, apparently cited as *Eriogonum sperguliunum* by Tietz 1972) (Polygonaceae) is possible, but records of *Gayophytum diffusum* (Onagraceae, Lembert 1894), *Oenothera binnis* (Onagraceae, Tietz 1972), and *Galium* (Rubiaceae, Klots 1951) are undoubtedly erroneous. *Lycaena* females (except *heteronea* Bdv. and *arota* (Bdv.)) land on the foodplant, crawl down the stem, and lay eggs on stems or trash at or near the base of the plant, which may account for their sometimes laying eggs on plants not eaten by the larvae. Shapiro (1974b) found that one California salt marsh population feeds on *Potentilla egedei* var. *grandis* and prefers to oviposit on this plant rather than on *Rumex crispus.*

The above foodplant record for *helloides* and *dorcas* suggests that if a population feeds on Polygonaceae it is *L. helloides,* but if it feeds on *Potentilla,* it may be either *L. helloides* or *L. dorcas.*

FOODPLANTS IN COLORADO

I found five species of Polygonaceae serving as hosts for high altitude Colorado *helloides:* 1) *Polygonum aviculare* (oviposition on base of stem at 13:35 standard time at Toll Ranch, 9400', Gilpin Co. Colo., 28 July 1977; oviposition on tiny plant next to *P. aviculare* and *Rumex acetosella* at 13:08, same locality and date). 2) *R. acetosella* (oviposition at base of stem 13:12, same locality and date). 3) *Polygonum douglasii* (oviposition on grass blade touching a *P. douglasii* stem 10:11, Jim Creek, 9400', Grand Co. Colo., 9 August 1977). 4) *Rumex densiflorus* (egg found on dead twig at base of plant, compared and found identical to eggs dissected from females, Keystone Gulch, 9600', Summit Co. Colo., 8 August 1977) (*L. helloides* eggs have a fairly smooth surface with cylindrical holes, whereas eggs of the sympatric *L. rubidus* (Behr) (the only other *Lycaena* present), *L. editha* (Mead), *xanthoides* (Boisduval), and *hyllus* (Cramer) are covered with peaklike bumps connected by lower ridges around the cylindrical depressions). 5) *Rumex triangulivalvis* (egg found on stipule at base of plant, 4 mi. SE of Fall River Reservoir, 10000', Clear Creek Co. Colo., 10 August 1977, egg identical to eggs from dissected females).

Potentilla fruticosa did not grow at the above sites, except for parts of the Keystone Gulch locality. The Keystone Gulch *helloides* often occurred near *P. fruticosa* and other *Potentilla* species, but females did not oviposit on *Potentilla* although both sexes often visited the flowers of *P. fruticosa* and other plants (*Erigeron speciosus* and *Achillea millefolium* frequently, and *Galium, Cirsium centaureae,* and *Potentilla* sp. occasionally). At other high altitude Colorado locations, I found *helloides* associated with *Rumex densiflorus* (near Weminuche Pass, 11000-11500', Hinsdale Co. Colorado) and *Rumex occidentalis* (Tennessee Pass, 10400', Eagle Co. Colo.). In Colorado, high altitude *helloides* are generally found along creeks where *Rumex* grows, or in valley bottoms where *Polygonum douglasii, P. aviculare,* and *Rumex acetosella* grow on gopher diggings.

At low altitude in Colorado, *helloides* is associated with *Rumex crispus* and *Polygonum pennsylvanicum* (near Canon City, 5300', Fremont Co. Colo.) The lower altitude *helloides* was found on *Rumex triangulivalvis* (an egg found on dead leaf below plant, slough 4 mi. E. Moffat, 7600', Saguache Co. Colo., 29 August 1977, identical to dissected eggs). *Potentilla* also is common in the sloughs at this Moffat locality, but *helloides* was found only where Polygonaceae occurred and was not found in pure stands of *Potentilla.*

Chambers (1963) found *helloides* associated with *Rumex* at Gunnison, Gunnison Co. Colorado (7680'), and reared larvae to adults on *Rumex crispus.* Another population at Gothic (10000') in Gunnison Co. was abundant in a field with no *Potentilla.*

The above foodplant records clearly demonstrate that high-altitude Colorado *helloides* feed on Polygonaceae, like *helloides* outside of Colorado, and not on *Potentilla* as does *dorcas* exclusively.

WING PATTERN

The key finding in resolving the taxonomy in the *dorcas-helloides* complex is that both are sympatric, synchronic (during the second brood of *helloides*), and do not intergrade over a broad area in northwestern Ohio, Michigan (Moore 1960), and southern Manitoba. *L. dorcas* and *helloides* must be treated as two separate species in this region. Populations elsewhere must be identified as one or the other according to whether they resemble *dorcas* or *helloides* from the Michigan region.

I examined series of both species collected 2 mi. No. of Highway 59, Livingston Co. Michigan, Fenton Road, 20 July 1971, by John Hafernik. At this locality *dorcas* occurs in the bogs around *Potentilla fruticosa,* whereas *helloides* occurs along roadside ditches associated with Polygonaceae. *L. dorcas* has one brood there, *helloides* three broods there.

L. dorcas and *helloides* differ in Michigan by eight wing pattern characters. They do not differ in male or female genitalia. These wing characters are described below, the differences between the species are noted, and the relation of high-altitude Rocky Mountain material to the Michigan populations is discussed. More than 600 individuals were examined.

The figure of *L. helloides* in Howe (1975), plate 55 fig. 13, is too dark ventrally to be an average representative of *helloides,* and the figures of "*dorcas*" plate 97 figs. 18 and 22, and "*cupreus*", plate 97 fig. 25, appear to be actually *helloides.*

1) Size. *L. dorcas* males average 12-13 mm forewing length, whereas Michigan *helloides* males (and males from Rocky Mountain high altitudes) average 14-15 mm. Females average about 1 mm larger than males from all localities observed.

The next five characters (2-6) are similar in males and females.

2) Forewing shape. *L. dorcas* has rounded wings, whereas *helloides* has more pointed forewings. Rocky Mountain material from all altitudes is clearly like *helloides,* with more pointed forewings.

3) Ventral hindwing red marginal band. *L. dorcas* has brown dots basal and distal to the red band between the wing veins, which accentuates the red band, whereas *helloides* lacks these brown spots bordering the red band. Rocky Mountain material from all altitudes clearly resembles *helloides* in this character, although an occasional specimen has a trace of these brown spots.

4) Position of the forewing postmedian black spots (ratio of the distance from wing base to postmedian spot in cell M_1 to length of forewing). *L. dorcas* has a smaller ratio which averages .68, versus .71 for *helloides.* Rocky Mountain material is again similar to *helloides*: low altitude (Lakewood, Jefferson Co. Colorado, 5500') specimens average .73, high altitude specimens (Keystone Gulch, Summit Co. Colo., 9600') average .71.

5) Color next to ventral hindwing postmedian spots. *L. dorcas* has the ground color darker medial than distal to the black spots, whereas in *L. helloides* the color is the same medial as distal. Rocky Mountain material is again most similar to *helloides;* ground color is the same basal as distal to the spots, except for occasional individuals from high-altitude populations which are similar to *dorcas.*

6) Ventral hindwing ground color. *L. dorcas* has the ground color purplish brownish ochre, whereas *helloides* has the color ochre to grayish ochre. Rocky Mountain material is closest to *helloides,* although at high altitude ground color is often darker.

The next two characters (7 and 8) have been used to assign populations to *dorcas* or *helloides.* However, I now show that both characters are too variable in high altitude Rocky Mountain populations to be really useful in assigning them to *dorcas* or *helloides*.

7) Male dorsal hindwing marginal band. In *dorcas* there is usually only one small red spot at the anal angle, whereas in *L. helloides* there is usually a complete red band of 4-5 spots. Table 1 gives the number of orange spots. Variation in this character is similar to that of the next so it will be discussed below.

8) Female dorsal color. *L. dorcas* is brown, sometimes with postmedian orange spots; it has very little sexual dimorphism. *L. helloides* has most of the forewing and the distal half of the hindwing orange except for a marginal border. Table 2 details this character. For both characters 7 and 8 there is considerable variation. Some *helloides* females from California are as dark as some *dorcas*. Most lowland western U.S. material is most similar to Michigan *helloides*. Higher altitude material is darker, including a subspecies from Broadwater, Cascade, and Sweetgrass Counties, Montana, and Yellowstone National Park, Wyoming, which has the dorsal orange of females replaced by whitish and the ventral hindwing red marginal band reduced. In Colorado, plains material is like Michigan *helloides*, as is material from the Arkansas River Canyon, Wet Mountain Valley, and San Luis Valley in southern Colorado (all of which have several broods). The lightest population in Colorado is from the floor of the San Luis Valley, 7600'. This valley is high, fairly cold, but dry, so that if light-dark phenotypes are environmentally determined in *helloides*, moisture in addition to temperature may affect the phenotype. High altitude (9000-11500') material from northern and central Colorado (the Front Range and Sawatch Range) averages darker than material from the San Juan Mountains in southwestern Colorado which in turn averages darker than material from the Sangre de Cristo and Wet Mountains in southern Colorado. Material from lower altitudes in northwestern, extreme western, and southwestern Colorado is intermediate between high altitude and lowland material.

The two wing pattern characters 7-8 are darker on the average in high altitude specimens, but they are variable (Tables 1-2), and I have never seen a Rocky Mountain *population* resembling *dorcas* in these two characters, although single individuals may do so. The dark individuals are always found to be part of a variable population including light individuals, and all Rocky Mountain populations and these dark individuals have their other characters (characters 1 to 6 above) resembling *helloides*.

DISCUSSION

9000' is the approximate boundary for voltinism in Colorado. Only one brood occurs in *helloides* populations above 9000', whereas two to three broods occur below 9000'.

L. helloides has a wide range, while *dorcas* may prove to be restricted to southeastern Canada and adjacent U.S., and perhaps northwestward to Alaska where Ferris (1977) lists *L. dorcas dorcas*. I have seen *helloides* from the Yukon in Canada. Ferris's (1977) *dorcas* subspecies *castro* (Reakirt), *megaloceras* (Ferris), *florus* (W. H. Edwards), and *arcticus* (Ferris) appear to all belong to *helloides*. Despite the very extensive overlap of the ranges of these four taxa with *helloides* shown on Ferris's maps (1977, Figs. 48,49), Ferris indicates that nowhere are they sympatric. He does, however, give many locations where "intergrades" and "introgressed populations" are found between *helloides* and these four taxa (Ferris 1977, p.35-36, 38). These difficulties of intergradation, introgression, and lack of sympatry between species caused by placing these four taxa into *dorcas* all vanish when it is realized that these four taxa actually belong to *helloides*. Some of the subspecies may result from darkening the wings or altering the phenotype due to temperature or humidity differences at high altitude or latitude. Ferris limits the subspecies *megaloceras* to the Bighorn Mts. Wyoming, but similar phenotypes with reduced hindwing submarginal orange lunules and whitish females occur more widely in Wyoming and southern Montana (Tables 1-2).

Ferris (1977) cites Coolidge (1924) to show that *helloides* winters as pupae (whereas *dorcas* winters as eggs), implying a biological difference between the species. Coolidge (1924) was probably wrong, however, because the preponderance of the evidence is that *L. helloides* over-winters as eggs. Shapiro (1974c) lists "larva or pupa" as the wintering stage of *helloides*, but later clarified his statement in a letter to me, stating that *helloides* probably over-winters as eggs, which hatch in late January in California. Chambers (1963) thought that his Gothic, Colorado, material wintered as eggs. Guppy (1964) specifically states that Vancouver Island, Canada, *helloides* spend the winter as eggs. Finally, all the *helloides* eggs from low and high altitude that I have found entered the winter without hatching.

CONCLUSION

High altitude Rocky Mountain *Lycaena* of the *dorcas-helloides* complex has as hostplants at least five species of Polygonaceae, the foodplant family used by *helloides,* rather than *Potentilla,* the hostplant of *dorcas.* Eight wing pattern characters which distinguish Michigan *dorcas* from Michigan *helloides* are, in high altitude Rocky Mountain populations, most similar to *helloides,* except for several wing pattern characters which are variable. High altitude Rocky Mountain populations are therefore *helloides,* not *dorcas.*

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Table 1. Number of orange lunules on margin of male dorsal hindwing. *—several generations per year; the other locations have only one generation per year (except perhaps the Minturn and Piney Creek locations in Colorado).

	Number of Lunules					
	0	1	2	3	4	5
A. *L. dorcas* (Michigan, Ontario)	3	11	3			
B. *L. helloides*						
*Michigan					1	3
*California				5	27	10
*Oregon, Washington				2	4	1
*lowland Nevada				1	9	9
Ruby Mts. Nevada		1		2	2	1
*lowland Utah, Idaho, Montana				1	3	9
*Twin Falls Idaho			3	3	5	3
mountainous Utah, Idaho, Wyoming, Alberta		3	1	5	4	1
subspecies with whitish females (Broadwater, Cascade, Sweetgrass Cos. Montana, and Yellowstone National Park Wyoming)		7		1		1
Colorado						
*plains (5000-6000')			1	6	41	64
*Wet Mtn. Valley and Salida (7000-8400')				2	16	17
*floor of San Luis Valley (Saguache Co.) 7600'						9
*mesas southwestern Colo. (La Plata Co.) 7500'		2	1	4	4	
*northwestern Colo.		1	2	1	4	
mountains Front and Sawatch Ranges	3	78	88	36	18	1
Minturn, Eagle Co., 8000'	2	6	5	4	4	
Piney Creek, Eagle Co., 7000'		5	8		3	
Keystone Gulch, Summit Co., 9600'		27	25	13	3	
Toll Ranch, Gilpin Co., 9400'	1	19	16	4	2	
Jim Creek, Grand Co., 9400'		7	9	2	1	
Arapahoe Pass Trail, Boulder Co., 11000'		5	4	3	1	
Fall River Res., Clear Creek Co., 10000'		3	5	5	1	
mountains Sangre de Cristo and Wet Mtn. ranges		3	23	25	9	1
West Creek Lake, Fremont Co., 11600'		1	5	3	1	
Ferguson Creek, Saguache Co., 9500'			4	4	3	
mountains San Juan range		6	8	5	3	
Weminuche Pass, Hinsdale Co., 11400'		3	2	1		
Spring Creek Pass, Hinsdale Co., 11000'		2	5	2	2	

Table 2. Extent of orange on dorsal forewing of females (A—completely brown; B—brown except for postmedian orange spots; C—postmedian band orange and some median orange spots; D—postmedian band solid orange and median part of wing mostly orange; E—orange except for basal third of wing and margin; F—completely orange except for darker wing base and margin.

	brown				orange	
	A	B	C	D	E	F
A. *L. dorcas* (Michigan, Ontario, Manitoba)	11	3				
B. *L. helloides*						
Michigan				1		
California		3	2	5	2	
Oregon, Washington			1	1		1
lowland Nevada			5	3	2	
lowland Utah, Idaho, Montana, North Dakota				2	1	2
Twin Falls Idaho			3	5		
mountainous Utah, Idaho, Wyoming, Alberta	1		3	3		
subspecies with whitish females (Broadwater, Cascade, Sweetgrass Cos. Montana, and Yellowstone National Park Wyoming)	1	2	5		1	
Colorado						
plains				3	16	6
Wet Mtn. Valley and Salida	3	1				
floor of San Luis Valley, Saguache Co.					3	9
mesas southwestern Colo. (La Plata Co.)		1	5	3	1	
western and northwestern Colo.			5			1
mountains Front and Sawatch Ranges	6	17	23	18	3	1
Piney Creek, Eagle Co.	2	2	3	1		
Keystone Gulch, Summit Co.	3	8	11	11	2	
Toll Ranch, Gilpin Co.		3	2	2	1	
Jim Creek, Grand Co.	1	2	2			
Arapahoe Pass Trail, Boulder Co.				1		
mountains Sangre de Cristo and Wet Mtn. ranges			5	4	8	
West Creek Lake, Fremont Co.			3	2		
Ferguson Creek, Saguache Co.			1	1		
mountains San Juan Range		4	6	10	2	
Weminuche Pass, Hinsdale Co.		3	6	9		
Spring Creek Pass, Hinsdale Co.					2	

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ON THE MEIOTIC CHROMOSOMES OF *ARGINA* SYRINGA CRAM

(ARCTIIDAE)

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ABSTRACT

The haploid chromosome number of *Argina syringa* was determined as 31 which forms the first report in this genus from India. The mean of the terminalization coefficient and chiasma frequency are .930 and .912 respectively.

CHROMOSOMES OF SOME INDIAN MEMBERS of the family Arctiidae, to which *Argina syringa* Cram here under study belongs, were reported by Gupta (1964), Rishi (1973) and Das and Nayak (1975). None of the three Indian representatives of the genus *Argina* (Hampson 1894) is known cytologically till to date and hence this note aims at recording the chromosome number and details of meiosis of *A. syringa* which forms the first report of chromosome number in the genus *Argina* from India.

All the material used for the present study was collected from the fields around A.U. Postgraduate Centre, Nallapadu, Guntur. Testes of adults as well as larvae were squashed in 2% aceticorcein without prefixation. The preparations were made permanent following the quick freeze method.

Counts on well spread metaphase I plates show clearly 31 bivalents (Fig. I), most of which are dumb-bell shaped with terminalized chiasma. Cross bivalents with single interstitial chiasma and ring bivalents with two terminal chiasma could also be seen in some bivalents.

Though the inherent difficulties with lepidopteran chromosomes like the large number, small size and almost isodiametric shape thwart detailed observations on their morphology, an attempt was made to study their meiotic features. Out of 7037 bivalents in 227 nuclei studied in 12 specimens, 430 were cross bivalents, 95 were ring bivalents, 5726 were dumb-bell shaped with terminal chiasma and 786 separated early into distinct univalents. The terminalization coefficient ranges from .867 to .960 with a mean of .930 and the chiasma frequency ranges from .813 to 1.089 with a mean of .912.

Comparison of chromosome number at different taxonomic levels in Lepidoptera reveals certain interesting affinities. Ray Robinson's review (1971) on this subject shows that 31 is the modal haploid number of the family Arctiidae and also that of the order Lepidoptera. The haploid number of *Argina syringa* Cram agrees with the modal number of the family and the order.

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Fig. I—Metaphase I stage of *Argina syringa* Cram.

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ANOTHER *ANTHOCARIS LANCEOLATA* X *A. SARA* HYBRID

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On April 12, 1970, we captured what we believe is a hybrid between *Anthocaris lanceolata lanceolata* Lucas and *A. sara* f. *reakirtii* Edwards. The locality was a steep, rocky, exposed S.-facing slope above Skelton Creek, 2800-3000′, along California riding trail 19E04.2, 1.1 air mi. due E. of Comet Mine, Sect. 23 & 24, T. 4 S., R. 19 E., E. of Jerseydale, ca. 10 air mi. NE of Mariposa, Mariposa Co., Calif. The canyon has extensive slate outcroppings with *Pinus sabiniana* Dougl.—*Quercus chrysolepis* Liebm.—*Aesculus californica* (Spach) Nutt. in association.

The specimen is a male in slightly worn wing condition taken late in the day near the bottom of the canyon along the horse trail. Both *sara reakirtii* and *lanceolata* were fairly abundant along the slope and creek bottom. Other pierids on wing at the time were *Pieris sisymbrii* Boisduval and *Euchloe hyantis* Edwards. *Pieris napi* f. *venosa* Scudder was also taken about 1½ mi. W. in a Ponderosa Pine forest.

The Skelton Creek specimen approaches *lanceolata* most strikingly in having a gray, densely mottled ventral surface and a somewhat similar mottling pattern, as well as a slightly pointed forewing apex. It also resembles *lanceolata* more than *sara reakirtii* in nearly lacking any black scales on the outer margin of the hindwing dorsal surface, which form bold-checkering in *sara reakirtii* at this locality. It resembles *sara reakirtii* in size, extensive black scaling at base of forewings, and the presence of the orange tips on the primaries, but the color of the "orange" is light, almost yellowish, rather than red-orange.

Comstock (1929) described a supposed male *A. lanceolata australis* (Grinnell) X *A. sara reakirtii* hybrid from Whitewater Canyon, Riverside Co., Calif., taken March 8, 1929 (leg. C. M. Dammers, LACM), as "dammersi". Our specimen compares fairly closely with his description and figure and with the color figure in Howe (1975), although it is not identical. Marked variation among hybrid butterflies is well-known. Three known *sara* aberrants (Comstock, 1927; Dornfeld, 1970) show no likeness to our specimen.

The specimen resides in the senior author's collection.

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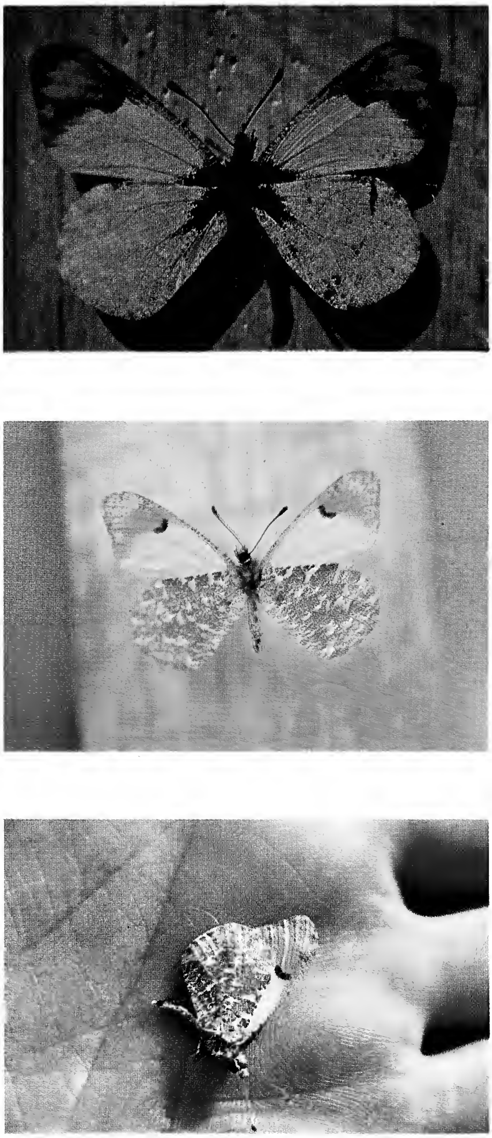

Fig. 1—*Anthocaris lanceolata* X *A. sara reakirtii* hybrid from Skelton Creek, dorsal surface.

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LARVAL FOODPLANT RECORDS FOR *PAPILIO ZELICAON* IN THE WESTERN UNITED STATES,

AND FURTHER EVIDENCE FOR THE CONSPECIFICITY OF *P. ZELICAON* AND *P. GOTHICA*

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INTRODUCTION

Following the description of *Papilio gothica* Remington (1968), several authors have questioned the validity of this entity. Clarke and Sheppard (1970) discussed the ecologic and genetic evidence presented by Remington and concluded that *gothica* is best considered a minor high mountain ecotype of *P. zelicaon* Lucas. Shapiro (1975) discussed the phenotypic plasticity of *zelicaon* in light of an analysis of the frequency of *gothica* and *zelicaon* characters in spring and summer samples of lowland *zelicaon* in California. He concluded that the seasonal phenotypic change, characteristic of a number of western North American species, in which a vernal phenotype of a multivoltine lowland population resembles the high elevation univoltine phenotype of the same species, applies also to *P. zelicaon,* and that Remington's characters were of little value in distinguishing *P. gothica* from the spring brood of California *zelicaon.*

This paper summarizes our own field work with *P. zelicaon* over a ten-year period. During the summer of 1967, we made detailed field studies of *P. gothica* in the vicinity of Gothic, Gunnison County, Colorado, the type locality. The same year and in subsequent seasons, we were able to document a number of foodplants for widespread populations of *P. zelicaon,* as well

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as make observations on voltinism in these populations. Our data lend further support to the concept that *gothica* and *zelicaon* represent the same species, as will be discussed below.

The foodplant records are documented in the Appendix in accordance with a method that we have previously described and used (Shields et al, 1969), and are summarized in the Table.

FOODPLANTS OF *P. GOTHICA* IN THE TYPE LOCALITY

In the description of *gothica,* Remington noted that all wild larvae (a total of five) taken by him and his assistants were found on *Pseudocymopterus montanus* (A. Gray) Coulter & Rose (Apiaceae). A search of three other apiaceous plants, namely, *Ligusticum porteri* Coulter & Rose, *Oxypolis fendleri* (A. Gray) A. Heller, and *Heracleum lanatum* Michx. (= *H. sphondylium* L.), failed to reveal immatures. No mention is made of other apiaceous plants growing in the area. Remington concluded that "*Pseudocymopterus* is surely the preferred wild host of *gothica* in Colorado."

We observed a single oviposition on *Pseudocymopterus montanus* near Crested Butte (6 air miles from Gothic). Following this, we repeatedly searched *P. montanus* plants in the vicinity of Gothic over a two-month period, but failed to find any *Papilio* immatures on it. However, searches of certain other apiaceous plants in the area revealed good numbers of *gothica* larvae. We found a total of sixty larvae on *Angelica ampla* A. Nels., six larvae on *Conioselinum scopulorum* (A. Gray) Coulter & Rose, and one larva on *Heracleum sphondylium.* In addition, we observed one oviposition on *Ligusticum porteri.*

We believe *A. ampla* and *C. scopulorum* to be the principal foodplants of *P. gothica* in the type locality, with *P. montanus, H. sphondylium,* and *L. porteri* serving as only occasionally used hosts. We found larvae common on *A. ampla,* relative to the foodplant biomass available. This large (flowering stems up to 2 m. high) umbellifer grows in wet meadows, often near streams. Along the East River below Gothic, we found *Papilio* larvae on the leaves of this plant with relative ease. Some plants yielded up to five or six larvae. We had a similar experience with *C. scopulorum.* This is a smaller (1 to 3 dm. tall) plant which also grows in wet meadows. Although larvae are much more difficult to locate on this plant due to the multi-dissected leaves which create a disruptive mottled shadowing, we were able to find six larvae in an area approximately 5 m. X 10 m. in 15 minutes. This contrasts sharply with the extensive time we spent searching plants of *P. montanus, L. porteri,* and *H. sphondylium,* only to note a single oviposition or larva on each of these. Furthermore, these latter three plants are common in the Gothic area, and present a larger biomass of potential foodplant than does either *A. ampla* or *C. scopulorum.* We found leaves of *A. ampla* and *C. scopulorum* both to possess a much stronger "parsley" odor when crushed than did leaves of *P. montanus, L. porteri,* and *H. sphondylium.* Perhaps ovipositing females are responding to this stronger olfactory stimulus, if human olfactory assessment is any measure of biochemicals important to the butterfly.

Remington also concluded that *gothica* prefers to oviposit on the flowerheads of the foodplant, while lowland *zelicaon* in California oviposits on both flowers and foliage, perhaps preferring the leaves. This was offered as an additional biological difference between *gothica* and *zelicaon.* However, all of the larvae we found on *A. ampla* were on the leaves of the plant, and most of these plants had no flowerstalks. The single ovipositions we observed on *P. montanus* and *L. porteri* were both on leaves, and the single first-instar larva taken on *H. sphondylium* was on a leaf of a non-flowering plant. Thus it appears that *gothica* may oviposit on either flowerheads or leaves, with an apparent preference for leaves.

RELATIONSHIP OF FOODPLANTS TO VOLTINISM OF *P. ZELICAON* POPULATIONS

The univoltinism of *P. gothica* was cited by Remington as another biological character distinguishing it from the multivoltine, lowland *P. zelicaon* of California. From our observations on California *zelicaon,* it appears that multivoltinism is primarily a characteristic of populations which feed on either the introduced *Foeniculum vulgare* L. (Apiaceae) or *Citrus* species (Rutaceae). *F. vulgare* provides some green foliage, flowers, or green seeds virtually twelve months of the year in most lowland areas. It often grows in vacant lots which are frequently cultivated in early summer for weed or fire control. The deep taproots of this perennial, unaffected by this superficial cultivation, sprout new foliage which is then utilized by later broods of *zelicaon* through the summer and fall months. *Citrus,* an evergreen subtropical tree, is available the entire year and *zelicaon* populations utilizing it are multiple-brooded (J. F. Emmel, unpublished data).

For low or mid-elevation populations on certain native apiaceous plants which remain green and succulent for four or five months, such as *Tauschia parishii* (C. & R.) Macbr., *Oenanthe sarmentosa* Presl., or *H. sphondylium,* there is a small percentage of pupae which do not diapause and emerge as a second brood. However, in other areas of lowland California, the native umbellifers used by *P. zelicaon* remain green just long enough to support a single generation of larvae. Examples of this type of foodplant are *Lomatium dasycarpum* (T. & G.) Math. & Const., *L. californicum* (Nutt.) M. & C., *L. marginatum* (Benth.) C. & R., and *L. utriculatum* (Nutt.) C. & R. in the North Coast Ranges and Sierra Nevada foothills. All of the pupae reared from larvae that we found on these *Lomatium* species went into diapause. Although the numbers we reared are too small to be statistically significant, it is not unreasonable to assume that at least some of these low-elevation, *Lomatium*-feeding populations are univoltine. By the time a second brood would be emerging, nearly all available foodplants would be turning brown and dying back, a distinct selective *dis*advantage for non-diapausing individuals. Thus in terms of voltinism, many lowland California populations of *P. zelicaon* probably do not differ from *P. gothica.*

Because Remington distinguished *gothica* from nominate *zelicaon,* it is of interest to speculate as to whether the type specimen of *P. zelicaon* was taken from a univoltine or multivoltine population; the type locality is merely given as "California" (Lucas, 1852). Remington apparently assumed that multivoltine *zelicaon* was nominate, but his basis for this assumption is not documented. At the time the type was collected (ca. 1850), the extent of introduced *Foeniculum vulgare* may have been very small indeed, and *Citrus* was not being grown on a large scale. The type, even if taken from a lowland area, could have been from a univoltine population. The development of the multivoltine, *Foeniculum*-feeding and *Citrus*-feeding ecotypes probably took place toward the end of the 19th century as these two foodplants became increasingly abundant. Obviously, much more field work and historical research needs to be done to determine more precisely the interrelationships of voltinism and foodplant usage in California populations of *P.*

zelicaon, as they exist now and as they were at the time *zelicaon* was named.

SUMMARY

1. Twenty-seven larval foodplants, in the families Apiaceae and Rutaceae, are documented for various populations of *Papilio zelicaon* in the western United States.
2. Field observations in the type locality of *Papilio gothica* indicate that at least five native foodplants are used, contrary to the statement in the original description of this butterfly that the sole foodplant is *Pseudocymopterus montanus.*
3. At low elevations in California, voltinism of *P. zelicaon* seems to be dependent on the nature of the foodplant(s) used by a given population. Many lowland populations are apparently univoltine due to the unavailability of green foodplant for a second generation, in spite of a long climatically favorable season. However, lowland populations utilizing certain other native foodplants with long-lived green leaves, or the introduced *Foeniculum vulgare* or *Citrus* species, are multivoltine.
4. These observations are interpreted as giving further support to the concept that *P. zelicaon* and *P. gothica* are conspecific, and that *P. gothica* is at best an ecotype of *P. zelicaon.*

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APPENDIX

Foodplant Records for *P. zelicaon*

As we consider *zelicaon* and *gothica* to be conspecific, no distinction is made between these two in listing the records. All foodplants are in the family Apiaceae (= Umbelliferae) unless otherwise noted. Abbreviations used for herbaria where voucher plant specimens are deposited are as follows: CAS, California Academy of Sciences, San Francisco; DHSU, Dudley Herbarium, Stanford University, California; RMBL, Rocky Mountain Biological Laboratory herbarium, Gothic, Gunnison Co., Colorado; RSABG, Rancho Santa Ana Botanic Garden herbarium, Claremont, California; UCB, University of California at Berkeley. Most plant determinations were confirmed by the following botanists: Nos. 1, 10, 13, and 22 by Mildred Mathias, University of California at Los Angeles; Nos. 2, 4, 5, 8, 11, 12, 14-21, 24-26, and 28 by Dennis Breedlove, CAS, and Lincoln Constance, UCB; Nos. 3, 6, 7, 27, and 29 by Richard Tilforth and Robert Thorne, RSABG. All specimens of *P. zelicaon* adults or immatures are deposited in the collection of the Los Angeles County Museum of Natural History. All observations of oviposition or collection of immatures were made by J. F. Emmel and O. Shields unless otherwise noted. Plant records are listed in alphabetical order to facilitate cross-reference with the listing in the table.

1. COLORADO: Gunnison Co.; near Brush Creek Cow Camp, along the East River below Gothic, 9000'; VII-24-67, 40 1st-3rd instar larvae taken on leaf uppersides of *Angelica ampla* A. Nels.; VIII-27-67, 20 4th-5th instar larvae taken on leaf uppersides of same plant species; approximately 20 larvae reared to pupae on leaves of this plant, all emerging in the spring of 1968. Plant material was collected (but not pressed) and found to be identical with a specimen of *A. ampla* in the RMBL herbarium, *D. Dunn 14,625,* collected along the East River below Gothic. Our plants also keyed out to *A. ampla* in Harrington (1954). This foodplant is somewhat local along the East River below Gothic, but immatures are easily located on the upper surfaces of the large, pinnately-dissected leaves. Some plants yielded up to six larvae. The majority of larvae were found on non-flowering plants.

2. CALIFORNIA: Siskiyou Co.; Caribou Lake, 6900', Trinity Alps; VII-22-68, 4 3rd-5th instar larvae taken on leaf uppersides of *Angelica arguta* Nutt. ex. T. & G., *J. F. Emmel 90,* UCB; larvae not reared. This plant is widespread in the mountains of northwestern California, and probably repre-

sents one of the major foodplants of *P. zelicaon* in this region.

3. CALIFORNIA: San Mateo Co.; San Bruno Mts., ravine 0.5 air mile W. of 1314' summit, 500'; VI-11-72, one 1st instar larva on leaf upperside of *Angelica hendersonii* C. & R., *J. F. Emmel 406*, RSABG; reared to pupa on leaves of same; pupa died several months later. (Observation by J. F. Emmel only)

4. NEVADA: Elko Co.; Thomas Canyon Campground, Lamoille Canyon, Ruby Mts.; VIII-7-67, 2 larvae on leaf uppersides of *Angelica kingii* (Wats.) C. & R., *J. F. Emmel 31*, DHSU; reared to pupae on leaves of same; adults emerged in April, 1968.

5. NEVADA: Humboldt Co.; Martin Creek Ranger Station, 7000', Santa Rosa Range; VIII-11-67, 5 1st-3rd instar larvae taken on leaf uppersides of *Angelica kingii* (Wats.) C. & R., *J. F. Emmel 191*, UCB; reared to pupae on leaves of same; one adult emerged in April, 1968; the remaining pupae died.

6. CALIFORNIA: Inyo Co.; Whitney Portal, 8200', east slope Sierra Nevada; VII-27-74, 2 4th-5th instar larvae on leaf uppersides of *Angelica lineariloba* Gray, *J. F. Emmel 527*, RSABG; both died before pupating (observation by J. F. Emmel only). This large plant is common along the eastern slope of the Sierra Nevada, and is suspected to be a major foodplant of *P. zelicaon* in this area. Bruce Griffin (personal communication) and Lloyd Martin (personal communication) have also collected *zelicaon* larvae on this umbellifer.

7. CALIFORNIA: Riverside Co.; Bay Tree Flat Campground, 5250', northwest of Lake Fulmor, San Jacinto Mts.; VI-23-76, 1 ovum on leaf upperside of *Angelica tomentosa* Wats., *J. F. Emmel 550*, RSABG; reared to pupa on leaves of same; adult emerged VII-13-76 (observation by J. F. Emmel only). This plant is abundant in local colonies at 4000' to 6000' in the San Jacinto Mountains but appears to be used infrequently by *P. zelicaon*. Searches of this plant in several previous years have failed to yield immatures.

8. COLORADO: Gunnison Co.; near Brush Creek Cow Camp, along the East River below Gothic, 9000'; VIII-27-67, 6 4th-5th instar larvae taken on leaves of *Conioselinum scopulorum* (A. Gray) C. & R., *J. F. Emmel 43*, DHSU; 2 reared to pupae on leaves of same; adults emerged in November, 1968. This plant is found in small, scattered colonies in wet meadows along the East River. We spent 15 minutes searching a 5 m. X 10 m. area where this plant was locally common to find 6 larvae. Larvae were difficult to see due to the mottled shade cast over them by the finely dissected leaves; the low growth habit of this plant allows surrounding vegetation to partially shield it and give further protective cover to the larvae. The ease with which we located larvae on this plant suggests that it is a preferred foodplant in the Gothic area.

9. CALIFORNIA: Riverside Co.; Hemet, 0.9 air mile WNW of peak of Reservoir Butte, 1715'; immature stages taken on *Foeniculum vulgare* L. (plant specimen not pressed, determined by J. F. Emmel) on the following dates: X-14-76, 2 5th instar larvae on leaves; I-17-77, 1 4th instar and 2 5th instar larvae on leaves; II-15-77, 10 ova on leaves; V-5-77, 31 ova on leaves; X-17-77, 17 1st-3rd instar larvae on flowerbuds, flowers, and fruit. (All observations by J. F. Emmel only)

10. COLORADO: Gunnison Co.; along the East River, below Gothic, 9000'; VII-24-67, one 1st instar larva on leaf upperside of *Heracleum sphondylium* L. ssp. *montanum* (Schleich. ex Gaud.) Briq.; reared to pupa on leaves of same; adult emerged XII-10-68. Plant material was collected (but not pressed) and found to be identical with a specimen of *H. lanatum* Michx. in the RMBL herbarium, *L. Ore s.n.* Our plants also keyed out to *H. lanatum* in Harrington (1954). Current nomenclature now treats North American *H. lanatum* as *H. sphondylium*. Because it has large, relatively

flat leaves, this plant is easily searched for *Papilio* larvae. It is common along streams in the vicinity of Gothic, and we were able to search large numbers of plants for larvae. Despite this, we noted only the single instance of a *P. zelicaon* larva on it.

11. CALIFORNIA: San Mateo Co.; San Bruno Mts., meadow 0.7 air mile N. of 1314' summit; VII-25-70, 1 3rd instar larva on leaf of *Heracleum sphondylium* L. ssp. *montanum* (Schleich. ex Gaud.) Briq., *J. F. Emmel 324,* CAS; reared to pupa on leaves of same; died within several weeks of pupation. Additional immature stages were taken as follows: IX-6-71, 1 ovum, 7 1st-2nd instar larvae on leaf uppersides, reared to pupae on leaves of same; 2 adults emerged in October, 1971, the remainder going into diapause; IX-25-71, 14 1st-5th instar larvae on leaf uppersides, not reared; X-31-71, 1 3rd instar larva on leaf upperside, not reared. (All observations by J. F. Emmel only.) *H. sphondylium* appears to be used primarily during the late summer and fall months in this locality when *Foeniculum vulgare,* widespread in the area and probably the principle foodplant of *P. zelicaon* here, is starting to dry up and become less attractive to ovipositing females. Repeated searches of *H. sphondylium* in this locality during the spring months over a five-year period failed to reveal larvae.

12. NEVADA: Elko Co.; rocky slope near the Jarbidge River, 2 miles S. of Pine Creek Campground, Jarbidge Mts.; VIII-10-67, 2 larvae on leaves of *Ligusticum grayi* C. & R., *J. F. Emmel 34,* DHSU; reared to pupae on leaves of same; one adult emerged in February, 1969, the other pupa died.

13. COLORADO: Gunnison Co.; Gothic, 9600'; VII-18-67, female observed to oviposit on leaf upperside of *Ligusticum porteri* C. & R. Plant material was collected (but not pressed) and found to be identical with a specimen of *L. porteri* in the RMBL herbarium, *M. E. Mathias 3418,* collected at Gothic. Our plant also keyed out to *L. porteri* in Harrington (1954). This plant is common in the area around Gothic, preferring somewhat dry slopes; it sometimes forms a dominant ground cover. We searched numerous individuals of this species, failing to find any larvae.

14. CALIFORNIA: Napa Co.; hills N. of road above confluence of Pope Creek and Maxwell Creek; IV-7-68, 3 1st-2nd instar larvae on leaf uppersides of *Lomatium californicum* (Nutt.) M. & C., *J. F. Emmel 55,* UCB; reared to pupae on leaves of same; one pupa died in 1969, 2 adults emerged in April, 1970. In this locality, this plant begins to die back in May, and succulent leaves would be unavailable for a second generation of larvae of *P. zelicaon.*

15. CALIFORNIA: Napa Co.; hills N. of road above confluence of Pope Creek and Maxwell Creek; IV-7-68, 4 2nd-4th instar larvae on leaves of *Lomatium dasycarpum* (T. & G.) M. & C., *J. F. Emmel 56,* UCB; reared to pupae on leaves of same; all pupae went into diapause, but three died the following year; 1 adult emerged in April, 1970 (observation by J. F. Emmel only). This *Lomatium* dies back sooner than does *L. californicum;* in fact, on the plants which produced larvae, some leaves were already turning brown on this date.

16. NEVADA: Lander Co.; lower end of Birch Creek Canyon, 6300', Toiyabe Range; VI-13-69, 8 4th-5th instar larvae on leaves of *Lomatium dissectum* (Nutt.) M. & C. var. *multifidum* (Nutt.) M. & C., *J. F. Emmel 160,* UCB; reared to pupae on leaves of same; all went into diapause; 1 adult emerged in February, 1970, and 1 adult emerged in February, 1971; the remaining pupae died during 1971-1972.

17. CALIFORNIA: Napa Co.; ridge 0.4 air mile NNW of Jct. of Butts Cyn. Road and Snell Valley Road, 800-1000'; IV-19-70, 12 ova and 1st-3rd instar larvae on leaves of *Lomatium marginatum* (Benth.) C. & R., *J. F. Emmel 265,* UCB; 3 reared to pupae on leaves of same, and all went into diapause; 1 adult emerged in May, 1971; the remaining pupae died in 1972. The leaves of this plant begin to die back in May, but it remains

green somewhat longer than does *L. californicum*, *L. dasycarpum*, and *L. utriculatum*. It seems doubtful that a second brood of *zelicaon* could utilize it.

18. NEVADA: Nye Co.; Troy Canyon, 7000', west slope of Grant Range; VII-7-69, 3 3rd-5th instar larvae taken on leaves of *Lomatium parryi* (Wats.) Macbr., *J. F. Emmel 182*, UCB; reared to pupae on leaves of same; 1 adult emerged in February, 1970; the remaining pupae died during 1970. This is an unusual foodplant for *P. zelicaon*, as it grows in a decidedly more xeric habitat than that in which *zelicaon* is usually found. We suspect that the primary foodplants of *zelicaon* in the Grant Range occur at slightly higher, moister elevations where more apiaceous species grow, and that *L. parryi* is used infrequently.

19. CALIFORNIA: Napa Co.; Table Rock, 2400', SE of Mt. St. Helena; IV-14-68, 6 ova on leaf undersides of *Lomatium utriculatum* (Nutt.) C. & R., *J. F. Emmel 58*, UCB; 3 reared to pupae on leaves of same; all pupae went into diapause; 1 adult emerged in April, 1969; remaining pupae died in 1970. The leaves of this plant die back during May and early June, preventing utilization by a second brood of *P. zelicaon*.

20. CALIFORNIA: Mariposa Co.; rocky slope above Skelton Creek, 2800-3000', near Jerseydale; III-29-70, female observed to oviposit at 12:48 p.m. PST on leaf underside of *Lomatium utriculatum* (Nutt.) C. & R., *J. F. Emmel 240*, UCB; ovum not reared.

21. CALIFORNIA: San Mateo Co.; San Bruno Mts., meadow 0.7 air mile N. of 1314' summit; VII-25-70, female observed to oviposit at 11:36 a.m. PST on leaf underside of *Oenanthe sarmentosa* Presl., *J. F. Emmel 323*, CAS. Additional observations: IX-6-71, female observed to oviposit at 11:38 a.m. PST on leaf underside; IX-25-71, 8 1st-3rd instar larvae on leaf uppersides, reared to pupae on leaves of same; 2 adults emerged X-30-31-71, remaining pupae went into diapause but died during 1972-1973; X-31-71, 1 5th instar larva on leaf upperside, reared to pupa, but died a few days later. (All observations by J. F. Emmel only.) Like *Heracleum sphondylium* in this locality, *O. sarmentosa* seems to be used by *P. zelicaon* primarily during the summer and fall months, when fewer "suitable" plants of the commonly used *Foeniculum vulgare* are available to ovipositing females.

22. COLORADO: Gunnison Co.; Crested Butte cemetery, 8900'; VI-22-67, female observed to oviposit on leaf upperside of *Pseudocymopterus montanus* (Gray) C. & R. Plant material was collected (but not pressed) and found to be identical to a specimen of *P. montanus* in the RMBL herbarium, *M. E. Mathias 3419*, collected at Gothic. Our plant also keyed out to *P. montanus* in Harrington (1954). *Pseudocymopterus* grows in dry meadows and on forested and open slopes, and seems relatively common around Gothic. We repeatedly searched plants of this species over a two-month period, but failed to locate any immature stages on it.

23. COLORADO: Montrose Co.; Warner Point, South Rim, Black Canyon of the Gunnison National Monument, 8000-8300'; VII-5-67, 2 2nd-3rd instar larvae on leaves of *Pteryxia hendersoni* (C. & R.) M. & C., *T. C. Emmel 17*, RSABG (plant material had been previously collected in this locality by T. C. Emmel in 1964); reared to pupae on leaves of same; adults emerged in March, 1968; VII-23-67, 1 1st instar larva on leaf upperside, reared to 4th instar and died.

24. NEVADA: Lander Co.; Kingston Canyon, 6600', Toiyabe Range; VI-13-69, 5 3rd-5th instar larvae taken on leaves of *Pteryxia petraea* (Jones) C. & R., *J. F. Emmel 154*, UCB; reared to pupae on leaves of same; all pupae went into diapause but died the following year.

25. CALIFORNIA: Mono Co.; slope 0.4 air mile S. of Slinkard Creek, 6000-6400', S. of Topaz Lake; VI-19-70, 3 4th-5th instar larvae taken on leaves of *Pteryxia terebinthina* (Hook.) C. & R. var. *californica* (C. & R.)

Math., *J. F. Emmel 321,* UCB; reared to pupae on leaves of same; pupae went into diapause, but died the following year. This is probably one of the major foodplants of *P. zelicaon* in the higher elevations of the Sierra Nevada. It has been established as a foodplant for this species at Donner Pass, Placer Co. (Emmel & Emmel, 1974), and at Kaiser Peak, Fresno Co. (Lloyd Martin, personal communication).

26. CALIFORNIA: Inyo Co.; Ruby Lake, 11,200', near Inyo-Fresno Co. line; VIII-4-68, 1 4th instar larva taken on leaf upperside of *Sphenosciadium capitellatum* A. Gray, *J. F. Emmel 107,* UCB; reared to pupa on leaves of same; adult emerged in April, 1969.

27. CALIFORNIA: Inyo Co.; Independence Creek, 4550', Owens Valley, WSW of Independence; VI-20-77, 2 5th instar larvae on leaf uppersides of *Sphenosciadium capitellatum* A. Gray, *J. F. Emmel 566,* RSABG; reared to pupae on leaves of same; 1 adult emerged VII-6-77, the other remained in diapause. (Observation by J. F. Emmel and T. C. Emmel). This plant retains green leaves well into August, and could serve as a host for a second brood of larvae.

28. CALIFORNIA: Riverside Co.; along Double View Drive, SW of Idyllwild, 5300', San Jacinto Mts.; VI-25-69, 2 3rd-4th instar larvae on leaf uppersides of *Tauschia arguta* (Nutt.) C. & R., *J. F. Emmel 171,* UCB; reared to pupae on leaves of same; one adult emerged VII-21-69; the other pupa went into diapause but subsequently died. One of us (JFE) has frequently collected *P. zelicaon* larvae on this umbellifer in the southern California mountains; it appears to be one of the major native hosts in this area. Some plants at higher elevations retain green leaves as late as August, and could support second brood larvae.

29. CALIFORNIA: San Bernardino Co.; near Sheep Creek wash, NE of Wrightwood, 5100', San Gabriel Mts.; VI-3-73, 2 4th-5th instar larvae taken on leaf uppersides of *Tauschia parishii* (C. & R.) Macbr., *J. F. Emmel 463,* RSABG; reared to pupae on leaves of same; adults emerged in the spring of 1974; VI-9-74, 4 ova on leaf uppersides; 2 reared to pupae; 2 adults emerged VII-6-74. (Both observations by J. F. Emmel and Bruce Griffin.) Many individuals of this *Tauschia* remain green and succulent well into late August, and are able to support a summer brood of *P. zelicaon.* James Haney (personal communication) has found *zelicaon* larvae on this plant along the eastern base of the Sierra Nevada, where it probably serves as a major foodplant.

30. CALIFORNIA: San Bernardino Co.; Redlands, at San Bernardino County Museum; VIII-10-77, 2 ova on new growth of Navel Orange, *Citrus sinensis* (L.) Osbeck (plant specimen not collected; determination by J. F. Emmel) (RUTACEAE); reared to pupae on leaves of same; adults emerged in August, 1977. (Observation by J. F. Emmel only).

31. CALIFORNIA: Riverside Co.; Hemet, 0.9 air mile WNW of peak of Reservoir Butte, 1715'; X-14-76, 1 5th instar larva on leaf upperside of new growth of Meyer Lemon, *Citrus limon* (L.) Burm. (plant specimen not collected; determination by J. F. Emmel) (RUTACEAE); reared to pupa on leaves of same; adult emerged in November, 1976; VIII-6-77, 6 ova on new leaves, reared to pupae on same; adults emerged in September, 1977; XI-10-77, 3 1st-instar larvae on uppersides of new leaves; reared to pupae in sleeve over leaves of same in garden, pupation occurring in mid-December; pupae went into diapause. One of us (JFE) has observed *P. zelicaon* adults flying in the *Citrus* groves around Hemet in every month from February to November, indicating that this *Citrus*-feeding population is multiple-brooded.

TABLE 1. FOODPLANTS OF *PAPILIO ZELICAON*

O = OVIPOSITION BY FEMALE ON PLANT OR OVA FOUND ON PLANT

L = LARVAE FOUND ON PLANT

FOODPLANT	LOCALITY	OBSERVATION
APIACEAE		
Angelica ampla A. Nels.	vic. Gothic, Gunnison Co., Colo.	L
Angelica arguta Nutt. ex T. & G.	Trinity Alps, Siskiyou Co., Calif.	L
Angelica hendersonii C. & R.	San Bruno Mts., San Mateo Co., Calif.	L
Angelica kingii (Wats.) C. & R.	Ruby Mts., Elko Co., Nevada Santa Rosa Range, Humboldt Co., Nevada	L L
Angelica lineariloba Gray	Sierra Nevada, Inyo Co., Calif.	L
Angelica tomentosa Wats.	San Jacinto Mts., Riverside Co., Calif.	O
Conioselinum scopulorum (A. Gray) C. & R.	vic. Gothic, Gunnison Co., Colo.	L
Foeniculum vulgare L.	Hemet, Riverside Co., Calif.	O, L
Heracleum sphondylium L. ssp. *montanum* (Schl. ex Gaud.) Briq.	vic. Gothic, Gunnison Co., Colo. San Bruno Mts., San Mateo Co., Calif.	L L
Ligusticum grayi C. & R.	Jarbidge Mts., Elko Co., Nevada	L
Ligusticum porteri C. & R.	vic. Gothic, Gunnison Co., Colo.	O
Lomatium californicum (Nutt.) M. & C.	Pope Creek, Napa Co., Calif.	L
Lomatium dasycarpum (T. & G.) M. & C.	Pope Creek, Napa Co., Calif.	L
Lomatium dissectum (Nutt.) M. & C. var. *multifidum* (Nutt.) M. & C.	Toiyabe Range, Lander Co., Nevada	L

Lomatium marginatum (Benth.) C. & R.	Butts Cyn., Napa Co., Calif.	O, L
Lomatium parryi (Wats.) Macbr.	Grant Range, Nye Co., Nevada	L
Lomatium utriculatum (Nutt.) C. & R.	Table Rock, Napa Co., Calif.	O
	Jerseydale, Mariposa Co., Calif.	O
Oenanthe sarmentosa Presl.	San Bruno Mts., San Mateo Co., Calif.	O, L
Pseudocymopterus montanus (Gray) C. & R.	vic. Gothic, Gunnison Co., Colo.	O
Pteryxia hendersoni (C. & R.) M. & C.	Black Canyon of the Gunnison, Montrose Co., Colo.	L
Pteryxia petraea (Jones) C. & R.	Toiyabe Range, Lander Co., Nevada	L
Pteryxia terebinthina (Hook.) C. & R. var. *californica* (C. & R.) Math.	Sierra Nevada, Mono Co., Calif.	L
Sphenosciadium capitellatum A. Gray	Sierra Nevada, Inyo Co., Calif.	L
	Owens Valley, Inyo Co., Calif.	L
Tauschia arguta (Nutt.) C. & R.	San Jacinto Mts., Riverside Co., Calif.	L
Tauschia parishii (C. & R.) Macbr.	San Gabriel Mts., S. Bernardino Co., Calif.	O, L
RUTACEAE		
Citrus sinensis (L.) Osbeck	Redlands, San Bernardino Co., Calif.	O
Citrus limon (L.) Burm.	Hemet, Riverside Co., Calif.	O, L

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THE ASSUMPTION OF ADAPTIVITY IN GENITAL MORPHOLOGY

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THE "LOCK AND KEY" HYPOTHESIS, first proposed by Dufour (1844), holds that the morphology of insect genitalia is an adaptive character which serves as a prezygotic reproductive isolating mechanism. This popular notion has long been used as a rationalization of the emphasis on genital morphology in taxonomic work, even though a functional explanation of a character's biological significance is not a necessary condition for its use in classification. The hypothesis was widely supported in the literature in the 1940s in the heyday of the "New Systematics," when there was tremendous interest in reproductive isolating mechanisms in general, and it found a place in such classic evolutionary syntheses as Dobzhansky (1951) and Mayr (1963). As Mayr noted, however, genital incompatibility would come into play as an isolating mechanism only after the waste of time and energy in courtship; thus it would tend to be superseded by other (behavioral, pheromonal) mechanisms which would act at an earlier stage. Rentz (1972) recently demonstrated that mechanical isolation can be an effective barrier to hybridization in katydids (Orthoptera: Tettigoniidae). However, other (ecological) factors comonly prevent interspecific courtships in nature.

The attitude of Lepidoptera taxonomists has been largely shaped by Klots (1933), who wrote in his landmark revision of the Pieridae that "changes in the genitalia must of necessity be . . . slowly effected . . . a change in the structures of one sex can only survive if there are corresponding changes in the structures of the other." Moreover, "The development of practically all of the external features . . . must be regarded as modifications to some degree controlled by the physical environment of the species. The development of the genitalia must be regarded as . . . nearly or entirely independent of such environment." These are powerful, deductive arguments for the conservatism of the genitalia, making them a very desirable and heavily weighted character in conventional taxonomy. However, a series of relatively little-known studies carried out in Germany casts Klots' arguments into very serious doubt, and with them the "lock and key" hypothesis as well.

H. J. Müller has carefully studied the phenotypic plasticity of the leafhopper genus *Euscelis* (Homoptera: Ciccadellidae). The "morphospecies" *E. plebeius* and *E. incisus,* which are "good species" by the conventional criteria of the "dead-bug taxonomist," were shown to be photoperiodically induced seasonal phenotypes of one species, and either could be produced from a brood of the other by environmental manipulation alone (Müller, 1954, 1957, 1961, 1965). This is hardly the first time biological information has overthrown a classification based solely on morphology, but it is of special interest because the genitalia were specifically at issue, and Müller was able to demonstrate that their morphology was in fact under photoperiodic control. In fact, aedeagus width, hitherto used as a taxonomic character in *Euscelis,* was shown to be an extremely sensitive index of developmental daylength (Müller, 1957). The dogma that the genitalia are insulated from environmental influences can no longer be sustained. Again, this is not terribly surprising: the developmental processes giving rise to various structures of an organism have to be coordinated in some way, even though some are more buffered against the external environment than others. More intriguing is Müller's determination that growth rate, and the durations of the nymphal instars, are independent of daylength. This implies that specific developmental processes are under photoperiodic control, and that seasonal disparities in genital morphology are not simply consequences of differences in growth rate. But are the genital variants somehow adaptive? If *E. plebeius* and *E. incisus* were good species as previously thought, they would be thought to be reproductively isolated by their differences. Does it make biological sense for the seasonal generations of a single multivoltine species to be isolated from one another?

Fortunately the problem has been solved. *Euscelis* was the subject of the most thorough study of the functional anatomy of insect genitalia ever published (Kunze, 1959). By studying pairs preserved *in copula,* Kunze was able to describe in minute detail how the parts of the male and female genitalia function in copulation, and how this function is affected by seasonal changes. A few quotes from Kunze highlight those findings which are relevant to the "lock and key" hypothesis.

> Only a loose morphological correlation exists between the male and female reproductive organs, albeit these organs do bear species-specific characteristics. A narrow, shape-determined correspondence, such as that between a complicated lock and its key, was not demonstrable. (p. 384)
>
> As anatomical study demonstrated, spring and summer generations of *Euscelis plebeius* differ considerably in the form and width of the penile shaft; they are largely similar, on the other hand, with respect to the formation and size of the female genital space. It follows . . . that the dimensions of the male and female copulatory organs . . . can vary within certain limits without reducing their functional capacity. This inference . . . may be confirmed relatively easily through mating of different seasonal forms, since spring and summer forms can be reared simultaneously, and differential copulatory behavior of the two forms was not observable.
>
> Supposing it to be the case that the morphological correspondence between the penis and the female genital space were as precise as that between a key and its appropriate lock, a successful copulation between different seasonal forms would be impossible, or at least greatly hampered. (Müller) carried out appropriate mating attempts between the two seasonal forms . . . the results of which he published in 1957. I have carried out similar tests . . . in order to control for the correctness of the anatomical data. . . . The findings confirm Muller's results. From them the following conclusion must be drawn: the shape of the penis in *Euscelis plebius* is not linked to its function in every detail; rather it can vary in rather large measure, without impairing successful copulation. (pp. 360-361)

Since the genitalia are so widely used in Lepidopteran taxonomy it is worth noting that Reinhardt (1969) has found morphological differences in the genitalia of the photoperiodically-induced seasonal forms of the common Palaearctic Nymphalid *Araschnia levana.*

In summary, the following points deserve consideration before blind assumptions are made regarding the function and taxonomic value of genital characters:

1. The assumption that interspecific differences in genital morphology function as a prezygotic reproductive isolating mechanism is unwarranted unless actual experimental or field evidence of inability to mate can be produced, as in Rentz's tettigoniid work, or the differences are of such a gross nature that copulation is unquestionably impossible.
2. Even if satisfactory evidence according to the criteria in (1) is forthcoming, this does not mean the genitalic difference is a

regular functional isolating mechanism in nature, let alone the only one. In most cases, close study demonstrates ecological or behavioral isolating mechanisms which keep the species apart long before attempted copulation.

3. Although the genitalia may be more conservative in time than many "superficial" characters, they are not insulated from environmental influences and may vary seasonally or otherwise as a consequence of direct developmental control or allometric processes. The *Euscelis* case demonstrates that without sophisticated knowledge of the functional anatomy of the genitalia of both sexes, the potential for reproductive isolation may be grossly misjudged, and erroneous taxonomic decisions may result.

4. Even in the absence of seasonal differences, large samples commonly reveal variability in genital characters which is comparable to that observed in "superficial" ones. With small samples, this variability may be incorrectly taken to have taxonomic significance. Descriptions of new taxa should whenever possible base genitalic data on more than a single preparation. This is of course merely good taxonomic practice and a deliberate avoidance of typology.

Butterfly taxonomy is undergoing a wave of splitting, a periodic phenomenon likely to be with us for a while. New taxa have been described in several groups, particularly the Lycaenidae, based on questionable genitalic characters. If biological data cannot be obtained it is incumbent on the taxonomist to continue to behave as if the biological species concept, and all the "population thinking" that goes with it, still applies. The dogma of the "lock and key" is dangerously typological.

ACKNOWLEDGMENTS

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NOTICES

NEW ADDRESS: The address of the Journal is now: c/o Santa Barbara Museum of Natural History, 2559 Puesta Del Sol Road, Santa Barbara, California 93105.

MAILING DATES: As of this issue, the mailing date of each number of the Journal will be listed in the Notice column, Volume 16, Number 3: December, 1977.

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The note "Type locality for *Calosaturnia walterorum* Johnson (Saturniidae)", which appeared in this journal (15(4): 214, 1977) was published by mistake, having been formally withdrawn from consideration by the *Journal of Research on the Lepidoptera* prior to its acceptance and publication in the *Journal of the Lepidopterists' Society* (29(3): 191, 1975). We regret this error.

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Ecology and Distribution of the Butterflies of Southern Central Colorado

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Abstract. — The 160 resident and 18 migratory species of butterflies occurring in an area west of Pueblo, Colorado, were studied. The area contains a great variety of habitats from alpine tundra to plains grassland. Spatial and altitudinal distribution, habitats, number and timing of broods, and larval and adult foodplants, were studied. More than 100 new larval hostplant records are presented. Diversity is greatest in the foothills, and decreases with altitude except that the plains have low diversity similar to the high mountains above 10000'. Distributions within the area are very consistent with altitudinal temperature gradients. Mountain barriers have not prevented the spread of butterflies to suitable habitats throughout the area. Postglacial warm periods apparently caused the extinction of alpine butterflies on Greenhorn Peak which is now above timberline. The area's butterflies are mainly western North American in distribution. Species composition differs somewhat from another mountain fauna just north of the area,due to an increased percentage of northern species there; both areas have similar percentages of eastern and western species. 109 of the 160 native species have only one brood per year. Time of flight is generally later at high altitude. Few one-brood species fly after July. At low altitude multi-brood species predominate. Ten populations differ in appearance from populations outside the area; these are described but not named. Most species in the Pueblo area occur in many plant associations. The most distinctive butterfly associations are those of the alpine zone and of riparian habitats. Other species are mostly restricted to pinyon-juniper woodland, *Cercocarpus* chaparral, or grassland habitats. Several species distributions are influenced by geological substrate. Most species often feed as adults, on flowers especially. Some species feed only on sap; several never feed as adults. Sap-feeding usually occurs as an alternative strategy for species which never feed on flowers.

Introduction

This paper is a study of the ecology and distribution of the butterflies of southern Colorado, specifically the southern half of the Pueblo 1:250,000 quadrangle (Fig. 1). Its purpose is to summarize our data on spatial and altitudinal distribution, number of broods and time of flight of these broods, larval and adult food sources, and to interpret these data. Studies of mate-locating behavior and flight patterns of the butterflies of this area were published elsewhere (Scott, 1976a, 1976b).

The data herein were gathered during 1961 to 1977. From 1961 to 1968 our sampling surveys were incidental to geological surveys by Glenn Scott. From 1969 through 1974 geological studies were intensified, and James Scott sampled areas and seasons missed during the geological surveys. We gathered more than 4,050 species-locality records, where a locality is defined as five miles or more from another locality, and more than 10,000 species-day records. Except for certain small areas such as the mountains west of Denver, this area has now the best studied Rocky Mountain butterfly fauna. The distribution data are worth reporting because previously very few species were known from the area (Brown et al. 1957), and because many species differ from those found in adjacent areas covered by that work. We present a biogeographic analysis of distribution within and near the area. Several examples of the effect of geological substrate on distribution are presented.

Along with sampling distributions, from 1967 to 1973 we gathered information on larval and adult food sources whenever possible. We found more than 100 records of larval foodplants based on observations of oviposition or larval feeding (most represent new insect-plant associations), and many hundred records of adult feeding sources.

Results

Resident and temporary immigrant butterfly species are listed below in systematic order. For each species, the following are listed: number of localities where it is known to occur (a locality is defined as a place more than 5 miles from another), type of geographic area occupied ("foothills" means the eastern side of the Wet Mountains from about 6000-8000'; "mountains" refers to the Wet, Sangre de Cristo, or La Garita Mountains), altitudinal limits, habitat, number of broods by dates (when precise days are given, these are average dates of start or end of a brood based on combined data from all years), variation with altitude, larval foodplants, and adult nectar sources. We list only larval foodplant specificity (a generalization of the detailed records) plus the records we have authenticated or discovered within the Pueblo area. Foodplant records will be fully documented in another paper. Abundances were arbitrarily rated from rare (few seen per year), uncommon (few seen per day), common (many seen per day), to abundant (many seen per hour). Place names are found on the map (Fig. 1) or on topographic maps of the United States Geological Survey. A few records cited by Nash (1893), Brown et al. (1957), and Cockerell (1890a, b, 1892a, b) are included.

Papilionidae

Parnassius phoebus. (sayii Edw. below timberline *hermodur,* H. Edws. above timberline) 33 localities: Wet and Sangre de Cristo ranges, 7000-13000'. One stray male was found near Westcliffe. Common in colonies in open grassland where *Sedum lanceolatum* abounds. One brood, June 18-August 2 (extremes May 26-Aug. 28) at about 9000' and early July-mid to late Aug. above timberline. Common to abundant. Adults feed often, mostly on yellow and white flowers including *S. lanceolatum* (the larval foodplant at Rosita; Scott 1973b) and on mud.

Papilio zelicaon nitra Edws. form *gothica* Rem. The black form nitra *does not occur here, 5 loc. in the mountains: along the west side of the Wet Mountains, the Royal Gorge, at Pass Creek and La Veta Pass, and west of the San Luis Valley, 5800-11000'. One brood, April 12-May 30 at lower altitudes, June 10-July 28 at higher altitudes. Uncommon. Larval hosts many Umbelliferae, associated with Harbouria trachypleura* on Pass Creek in Huerfano Co. *Papilio* adults often feed on flowers (especially bluish ones: *Cirsium, Medicago, Cleome, Monarda,* etc.) and mud.

Papilio polyxenes. asterias Stoll. 27 loc: throughout the area including the San Luis Valley floor, from 4300-9500' (and seen above timberline). Occurs in a variety of habitats (grassland, pinon-juniper, cities). Three broods on the plains, May 22-June 18, July 13-Aug. 16, and Sept. 2-Oct. 22; one brood in the mountains June 26-Aug. 27. Uncommon. Larval hosts are many cultivated and wild Umbelliferae.

Papilio bairdii Edw. 35 loc: plains (east of Canon City and Florence), Wet Mtn. foothills (Soda Gulch), Arkansas River Canyon (Royal Gorge to Nathrop) where it occurs within a few miles of the river but as far away as Hillside, and low hills on the west & south side of the San Luis

Valley. 4600-9600' (rare above 8000'). Pinon-juniper habitat in the last two areas. One small brood May 3 (plains) to mid June, a second larger flight late June to late August (peak July 30) which may represent two broods. Uncommon to rare in most years, common in 1965. Larvae feed on *Artemisia dracunculus* (larvae raised to adults from Canon City and Salida). Phenotypic variation is great; black forms ("*bairdii* ") were 73%, yellow forms ("*brucei* Edw.") 27%, of a large sample. Width of yellow bands of both forms in extremely variable, as are other characteristics. The side of the abdomen of black forms varies from solid black with yellow spots, to partly yellow; about a fourth of black forms, usually males, have some degree of abdominal yellow suffusion, and 2.5% of black forms (all males) have the side mostly yellow (form "*hollandii* Edw."). These percentages of forms are similar throughout the area.

P. glaucus rutulus Lucas. 49 loc: throughout the area except the San Luis and Wet Mtn. Valley floors, from 4800-10436' (usually below 9000') in riparian habitats. One brood, early June to mid July plains-foothills, to late July elsewhere (extremes May 29-Aug. 31) although rare late records may represent a partial second brood. Usually uncommon. Larval hosts *Salix* (larvae raised to adults at Pueblo), *Populus*, *Fraxinus* in California (A. Shapiro, written communication 1974), and perhaps also *Alnus*, *Betula*, and *Ptelea baldwinii*. *P. g. rutulus*, *P. eurymedon*, and *P. multicaudata* sometimes congregate at mud. *P. glaucus* and *P. g. rutulus* are provisionally treated as subspecies because they intergrade in British Columbia (Scott & Shepard 1976). Also, it has not been appreciated that *P. glaucus canadensis* is intermediate in wing pattern and biology between *glaucus* and *rutulus*. *P. g. glaucus* from West Virginia refuses *Salix* which *glaucus canadensis* in New England and *P. rutulus both feed on in nature.*

P. multicaudata Kirby. 36 loc: throughout the area except the Wet Mtn. and San Luis Valley floors, 4860-9100' (usually below 8000'), mainly in drier canyon bottoms than *P. g. rutulus*. Apparently two broods at low elevations, mid April to late May, mid June-early Aug. Apparently only one brood higher in the mountains, mid June-early Aug. Uncommon-common. Larval hosts Rosaceae: *Prunus* including *P. virginiana* and *P. americana*, *Amelanchier*; Oleaceae: *Fraxinus*; Rutacea: *Ptelea baldwini.*

P. eurymedon Lucas. 3 loc.(?): Juanita Scott found a dead male beside the road on the west side of the Sangre de Cristo Mts. west of

La Veta Pass near Russell (June 21, 8700'). Nash (1893) recorded the species from Rye (6800') in the Wet Mtn. foothills, and A. Detmar caught a worn specimen at Greenleaf Creek on the east side of the Sangre de Cristo Mts. (Aug., about 8800') which he discarded before I could examine it. Probable Arkansas Canyon and Huerfano Park. 6800-8800', in mountainous areas. One brood, usually June-July elsewhere. Rare in this area, and some or all of the three records may be erroneous. Larval hosts *Ceanothus fendleri*, *Crataegus*, *Ribes*, *Holodiscus*.

P. cresphontes Cram. Strays from farther south were found at Rye (Denver Museum of Natural History collection) and Pueblo (Brown et al. 1957).

Battus philenor (Linn.). Strays were found at Pueblo, Rosita, Hardscrabble Canyon (Nash, 1893), Rye (Denver Museum collection), and Round Mtn. (Art Detmar). The species is not native, although it is known to breed temporarily in Colorado on cultivated *Aristolochia* (Brown et al. 1957).

Pieridae

Anthocaris sara Lucas. 5 loc: along both sides of the Sangre de Cristo Mts. (Hayden Creek Campground, near Poncha Pass, W. of Hayden Pass) and the mountains west of the San Luis Valley, probable in Wet Mts., 8000-10500', in semi-forested valley bottoms. One brood, late May-late June. Uncommon, sometimes common. Larval hosts many Cruciferae. Adults of *Anthocaris*, *Euchloe*, and *Pieris* often feed on flowers of all colors, most often yellow and white ones, especially Cruciferae.

Euchloe ausonia coloradensis (H. Edw.). 33 loc: throughout the mountains and plains-foothills ecotone from 6150-10300', in open areas. One brood, mid April-June 12 in Wet Mtn. foothills, late May-early July at higher altitudes (as late as July 30 at the highest altitude). A partial second brood in early July occurred once in Jefferson County. Common. Larval hosts many Cruciferae (Scott 1974c). *E. ausonides* is a subspecies of *E. ausonia* (Higgins & Riley 1970).

E. olympia (Edw.). 17 loc: plains (Pueblo, etc.), Wet Mtn. foothills, Arkansas Canyon (Royal Gorge and Cotopaxi), probable Huerfano Park, 4800-6800', in open areas. One brood April 9-May 21. Uncommon, sometimes common. Larval hosts Cruciferae.

Pieris napi macdunnoughii Rem. 32 loc: throughout the mountains from 6700-11000', especially above 8000', in moist areas along streams. One brood, late June-early Aug. (extremes May 29-Aug. 12). Uncommon to common. Larval hosts many cruciferae.

P. rapae (Linn.). 26 loc: plains, Wet Mtn. foothills, Arkansas River Canyon near the river, San Luis Valley floor, and three records from the Sangre de Cristo Mts. (Hermit Pass road 9000', Medano Creek, and west of Hayden Pass 8800'), from 4300-9000', in towns and in natural riparian habitats. Multiple broods on the plains, flying continuously from early April to early Oct. Two or three broods in the Arkansas Canyon, late May to mid June, early July-early Sept. July 15-Aug. 14 in San Luis Valley (a first brood may occur there). Common in cities, usually uncommon in native habitats. Larval hosts many Cruciferae, rarely on Capparidaceae.

P. sisymbrii elivata (B. & B.). 24 loc: Wet Mtn. foothills, extending out onto the plains as far as 2 mi. NE Crow and 2 mi. E. Penrose, the Arkansas Canyon, San Luis Valley (Villa Grove), hills in Huerfano Park, and reported in Wet Mountain valley in "W. Custer County" (Cockerell in Nash, 1893), and 11 mi. NE Silver Cliff (Brown et al. 1957), from 5200-8600' in fairly open habitats. One brood, April 7-late May, seldom to mid June. Usually uncommon. Larval hostplants Cruciferae.

P. chloridice beckerii Edw. 25 loc: plains, Arkansas Canyon, Huerfano Park floor, and San Luis Valley floor, 4860-8200', mostly in arid eroded habitats. About 4 broods on the plains, with the last broods coalesced: April 9-May 2, June 3-22, July 5-October. In the Arkansas Canyon there are probably three broods, of which the second is June 15-July 10 and the third is Aug. 15-Sept. 10. Sometimes common on the plains, uncommon elsewhere. Larval hosts many Cruciferae including *Stanleya pinnata* (two ovipositions west of Pueblo) and Capparidaceae (a genus not in Colorado). *P. beckerii* is a subspecies of *chloridice* (Higgins & Riley 1970).

P. protodice Bois & LeConte. 55 loc: throughout the area 4300-12349', mainly in open areas. There are perhaps four broods on the plains with the first brood (*vernalis*) from early April to mid May, many records from late May through September, and *vernalis* again in late Sept.-Oct. In the mountains there are perhaps three broods from April to September. It probably does not breed much above 9000' and the few individuals above this apparently arrive from lower altitudes. Larval host Cruciferae including *Sisymbrium altissimum* (oviposition at Howard), *Thelypodium elegans* (oviposition at Box Canyon), *Descurainia sophia* (oviposition at Bear Creek, Fremont County), *D. pinnata* (oviposition at Crow, Pueblo Co.), *Thlaspi arvense* (oviposition at Coaldale) and on Capparidaceae including *Cleome serrulata.*

P. callidice occidentalis Reak. 18 loc: throughout the mountains, and one record on the plains (Low Back Creek SE of Florence), only one record Wet Mtn. foothills (Hardscrabble Can.), few records Arkansas Canyon (Monarch, Salida, Coaldale), from 5600-13800' (only two records below 7000', usually above 8000'). There is apparently only one brood in the foothills, April 9-late May (form *calyce*), one and sometimes a partial second brood at higher altitudes, mid June-mid Aug. (extremes May 29-Sept. 10, the last date *calyce*). The form *calyce* occurs during summer mainly above timberline (one record below 10700') along with typical individuals which may fly up from lower altitude. Uncommon, sometimes common above timberline. Larval hosts many Cruciferae, occasionally Capparidaceae. *P. occidentalis* is a subspecies of *P. callidice* (Brown et al. 1957, Higgins & Riley 1970).

Neophasia menapia (F. and F.). 19 loc: throughout the mountains, 6300-8800', in pine forests. One brood July 16-Sept. 2. Uncommon to common. Larval foodplants conifers including Pinus, *Pseudotsuga menziesii, Abies. P. ponderosa* and *P. edulis* prevail where the species occurs in this area. Adults feed on many flowers such as *Cleome, Rudbeckia, Solidago,* especially during cloudy periods when they come down from the trees.

Colias cesonia (Stoll). Strays have been caught at 15 localities throughout the area except the San Luis Valley, from 4300-10000', usually flying rapidly along valley bottoms, from May 10-Aug. 12 (representing several broods farther south). The species was fairly common and fresh in Hardscrabble Canyon in July 1973, suggesting temporary local breeding. Larval hosts are legumes. *Colias* adults feed on many flowers of all colors, perhaps most often on bluish or reddish blue ones, and on mud where they may congregate.

C. meadii Edw. 18 loc: Wet Mts. (Greenhorn Peak to Ophir Creek), Sangre de Cristo Mts., and the Cochetopa Hills west of the San Luis Valley, from 10000-13600', in meadows and tundra, from July 12-Aug. 25 (extremes June 23-Sept. 3). Common, sometimes abundant. Larval hosts are legumes, including *Trifolium dasyphyllum* (ovipositions seen at Hermit Pass, Baldy and Greenhorn Peaks).

C. eurytheme Bois. and *philodice* Godart. 55 loc. (*eurytheme*) and 66 loc. *(philodice):* throughout the area from 4300-12500' (more frequent below 9000') in open hillsides, meadows and agricultural legume fields, etc. Perhaps four broods on the plains and foothills from mid April through October, perhaps two or three broods in the mountains from late May to early September. *C. philodice* is commoner than *eurytheme* throughout the area, and is sometimes abundant in alfalfa fields and meadows with *Trifolium*. In 42 of 80 loc. both species are known; there appears to be no ecological or temporal separation of these two entities in this area, and phenotypic intermediates sometimes occur more frequently than the low *eurytheme* frequency. Larval hosts are many legumes: for *eurytheme*, including *Trifolium nanum* (oviposition at Hermit Pass), *Medicago lupulina* (oviposition at Five Points Recreation Area, Fremont Co.), *Mellilotus officinalis* (oviposition at Beulah); for *philodice*, including *Astragalus* spp. (ovipositions NE of Rosita and in Saguache Park), *Trifolium* sp. (oviposition Ophir Creek, Custer Co.), *Oxytropis* sp. (oviposition Saguache Park).

C. alexandra Edw. 44 loc: throughout the mountains (a two-brooded plains ecotype found southeast of Denver does not occur here) from 6800-10300', usually in open grassy areas. One brood late June-mid Aug. (extremes June 14-Aug. 26), slightly earlier (mid June-mid July) in the foothills. Common. Larval hosts legumes including *Astragalus* (H. W. Nash observed oviposition at Rosita).

C. scudderii Reak. 3 loc: Wet Mts. and Sangre de Cristo Mts. (near Micawber Mine, western Custer Co., Cockerell 1890a), from 10300-11000', in willow bogs. One brood mid July-mid Aug. (extremes June 27-Aug. 25). Uncommon to common. Larval hosts are bog *Salix*.

Nathalis iole Bois. 49 loc: throughout the area (but only two loc. in SanLuis Valley) 4300-13000' (usually below 9000', more common at low altitudes) in open areas often flying along valley bottoms. Several broods, mid June-early October (extremes May 25-Oct. 22) plains, June 14-Aug. 10 Arkansas Canyon, July 4-Aug. 25 in Wet Mtn. Valley. Usually uncommon, but is common in some years, especially in late summer; the data strongly suggest that the species is very mobile, probably migratory. Larval hosts include many Compositae: *Bidens*, *Helenium*, *Thelesperma*, *Dyssodia "papposa"* (Nash, 1893), *Boebera*; Caryophyllaceae: *Stellaria media*; Geraniaceae: *Erodium* (dubious); Rubiaceae: *Galium* (Forbes 1960; dubious). Adults feed on various low flowers, often yellow ones.

Eurema nicippe (Cram.) 17 loc: throughout the area (4300-12500'), often flying along valley bottoms, from June 4-Aug. 6, one record Sept. 10. Rare, a migrant from farther south. Larval hosts are legumes. It may occasionally breed here; several individuals were seen at one locale, and a colony existed at another locale.

E. mexicana (Bois.) 9 loc: throughout the area except for the San Luis Valley and Huerfano Park, 6000-12000', May 30-Sept. 6 (mostly June 11-Aug. 2). Rare, a migrant from farther south, although it may temporarily breed in Colorado, because several individuals were seen at each of several localities. The specific legumes that are known as larval foodplants do not occur in Colorado.

E. nise (Cram.) We caught a stray female of this Texas species on the upper plains north of Goodpasture, Aug. 1.

Phoebis sennae (Linn.) ssp. 3 loc: Arkansas Canyon and Wet Mtn. Valley (Rosita, Cockerell 1927), 7000-9000', June 26 to July 24, represent strays from farther south. Larvae feed on legumes.

P. philea (Johansson). One stray was found in the San Luis Valley (Brown et al. 1957).

Kricogonia lyside, (Godart). One specimen in foothills (Phantom Canyon, Aug. 16, Maurice Howard) was a stray from farther south.

Nymphalidae

Danaus plexippus (Linn.) 27 loc: throughout the area from 4300-11500' (rare above 9000'), mainly in lowlands near the larval foodplants. There are scattered records from April 30-June 9, and Sept.-Oct., but most records are from June 26-Aug. 26. This migratory species can be common locally. Larval hosts many *Asclepias* and rarely Apocynaceae. Adults feed on *Asclepias* and other flowers of various (usually bluish or reddish blue) colors.

D. gilippus strigosus (Bates). 11 loc: throughout the area (probable in Huerfano Park) from 4300-9200', from June 14-Sept. 22 (it has multiple broods farther south where these strays originate). A rare migrant. Larval hosts Asclepiadaceae.

Agraulis vanillae incarnata (Riley). 4 loc: plains, Arkansas Canyon, and Wet Mtn. Valley from 4300-9000', mostly flying in valley bottoms, from May 24-Aug. 6. A rare migrant. Larval hosts (*Passiflora*) are not native to Colorado.

Anaea andria Scud. 9 loc: plains west to Canon City and the mouth of Phantom Canyon, from 4300-6200', mainly in Cottonwood-willow

Anaea andria Scud. 9 loc: plains west toCanon City and the mouth of Phantom Canyon, from 4300-6200', mainly in Cottonwood-willow groves along streams. Two broods: June 29-Aug. 17, then Sept. 13-April 14 (apparently overwintering). Uncommon. Larvae feed on *Croton texensis* (Euphorbiaceae) (oviposition in Baca County, many leaf-rolling larvae from near Canon City raised to adults). Adults never feed on flowers, but often on willow and popular sap, sometimes on mud.

Asterocampa celtis (Bois. & LeConte) *ssp.* 7 loc: lower foothills (Oak Creek) and plains, 4300-6800', on or near the larval host which grows in valley bottoms. Apparently two broods, June 17-July 24, Aug. 3-Sept. 15 (extremes June 13-Oct. 25, peaks in late June and Late Aug.). sometimes common in Denver, Colorado. Larvae feed on *Celtis reticulata* (Ulmaceae; many ovipositions on twigs and leaves near Rockvale). *Ulmus parvifolid* was suspected as a foodplant at Denver, but first instar larvae would not eat the leaves. Adults rarely feed on flowers (*Jamesia,* etc.) but often feed on sap especially of willows occasionally feed on mud or on *Rubus* berries.

Limenitis bredowii eulalia (Dbdy). One stray female from farther south was found in the foothills north of Goodpasture, Aug. 1. Larvae feed on oaks, which are abundant in the vicinity.

L. archippus archippus (Cram.) 12 loc: plains (west to Canon City) and all over the floor of the San Luis Valley (strangely absent in Arkansas Canyon), probably in Huerfano Park, 4300-7750'. Individuals fly beside the foodplant along streams and ditches. Two broods on the plains, May 19-July 5, July 24-Sept. 7 (extreme Oct. 7); perhaps only one brood in San Luis Valley, June 13 (south of this area) and July 19-Aug. 9. Uncommon, sometimes common. Larvae feed on Salicaceae, including *Salix exigua* which is certainly the main or only food in this area. Adult *Limenitis* feed on many flowers of all colors (often bluish or reddish blue), occasionally on sap.

L. weidemeyerii Edw. 57 loc: throughout the mountains, and the plains east to Pueblo, 4860-10500' (rare above 9000'), mostly in valley or gulch bottoms. Perhaps two broods (or one long brood) on the plains and Arkansas Canyon, June 8-Sept. 2, one brood in the Wet Mountain and San Luis Valleys, June 24-Aug. 9. Fairly common. Larval hosts Salicaceae; including *Salix*, *Populus tremuloides*; Rosaceae: *Amelanchier alnifolia*, *Holodiscus*.

Precis coenia (Hubn.) 6 loc: plains, Wet Mtn. foothills (Beulah, Nash 1893), and Wet Mtn. Valley (Rosita, Nash, 1893), 4300-9000', usually near *Plantago* along streams. It is a rare stray here, but may breed temporarily such as in 1971 when 6 individuals were caught. Larval foodplants are various Plantaginaceae, Scrophulariaceae, and Verbenaceae (*Lippia*) (Scott 1975c). Adults feed on flowers of many colors and on mud.

Polygonia interrogationis (Fab.) 3 loc: plains (Pueblo, Canon City) and Wet Mtn. foothills (Hardscrabble Canyon), probable in Huerfano Park, 4300-5400', along streams and in popular groves, and in suburbs. There are probably two broods, the first June 10-July 6, the second (or part of the first) from July 19-mid Aug., the third (or second) from late Aug. hibernating to the next April-May. Rare-uncommon. Larvae feed on three closely related families — Urticaceae: *Urtica*; Ulmaceae: *Ulmus parvifolia* (many larvae raised at Pueblo by M. Howard), *Celtis*; Moraceae: *Humulus*. *Polygonia* adults often feed on sap, sometimes on *Rubus* berries, sometimes on flowers, especially yellow ones, occasionally on mud.

P. satyrus (Edw.) 21 loc: throughout the area between 5100-8000', on the plains to east of Florence (a sight record eastward in Baca County) along streams and in poplar groves. Records occur continuously all year, but there are apparently two broods, the first June 24-Aug. 3 (rarely Aug. 27), the second September overwintering to early June. Uncommon. Larval hosts Urticaceae: *Urtica gracilis*; Ulmaceae: perhaps on elm (no documentation exists); Moraceae; *Humulus lupulus*.

P. zephyrus (Edw.) 64 loc: throughout the mountains including hills just east of the mountains, and hills in the San Luis Valley and Wet Mtn. Valley floors, 5800-13000' (usually below 10000') in gullies and valley bottoms. Two broods, the first from June 17-Aug. 4, the second Aug. 25 overwintering to late May (some adults may be found throughout the year). Perhaps only one brood near timberline, July 6-Aug. 16 then perhaps overwintering. Common. Larval hosts *Ribes* (Saxifragaceae).

P. faunus hylas (Edw.) 19 loc: all three mountain ranges (probable in Huerfano Park) from 6800-11000' (usually 8000-10000'), along streams. One brood, from Aug. 10-overwintering to late May (extremes Aug. 2 to July 3). Uncommon around the San Luis Valley, sometimes common elsewhere, rarely very abundant on yellow flowers in August (individuals apparently do not mate until spring). Larval foodplants Salicaceae (*Salix*) in Colorado. Other recorded hosts are *Rhododendron*; Corylaceae: *Betula*, *Alnus*, which are possibly correct, and *Ribes* which seems dubious or confused with other *Polygonia.*

Nymphalis antiopa (Linn.) 45 loc.: throughout the area 4300-11000', in riparian habitats. Two broods, June 24-mid Aug., late Aug. overwintering to late May (some individuals occur all year). Common. Larval hosts Salicaceae: *Salix* including *S. exigua* (larvae from Lake Creek Campground, Custer Co., and Mirage, Saguache Co., reared to adults), *Populus*; Ulmaceae: *Ulmus*, occasionally *Celtis reticulata*; Moraceae: *Humulus lupulus*; other recorded hosts are *Betula*, and, doubtfully, *Rosa* and *Pyrus communis* (pear). Adult *Nymphalis* occasionally feed on flowers of all colors (often yellow), but more often feed on willow and cottonwood sap, rotting fruit, and occasionally on mud.

N. milberti (Godart) *ssp.* 50 loc: throughout the area (infrequent on the plains where it extends east to Pueblo), 4860-13800', frequent and widespread above timberline, often near *Urtica* or on hilltops at low elevations. Its presence above timberline (*Urtica* does not grow there) is puzzling and may involve its dispersal. Two broods, June 21-mid Aug., late Aug. overwintering to late May (some individuals may be found all year). Perhaps one overwintering brood above 10000' (records June 15-Aug. 25). Uncommon, sometimes common above timberline or around *Urtica*. Larval hosts *Urtica dioica gracilis* (larvae from Texas Creek and Hillside raised to adults); Ulmaceae: *Ulmus* occasionally. Adults often feed on flowers, especially yellow ones.

N. californica (Bois.) 12 loc: over the Wet Mts., and the east side of the Sangre de Cristo Mts. (North Taylor Creek). Probable throughout the mountains (present farther south along the Rio Grande River), from 6800-10700' (once 12349'), on hilltops and valley bottoms. Two broods, June 29-early Aug., Sept.-late May. Rare to uncommon. Larvae feed on *Ceanothus*.

Vanessa cardui (Linn.) 60 loc: throughout the area, 4300-13000'. Individuals migrate north to the area in April-May, breed several generations (records occur throughout the summer but are most frequent in late June and in late July-early August), then fly south in Sept.-Oct. Records occur every year from 1965 to 1973 except for 1967. An immense northward flight occured May 1973 and a small return flight was noted in Sept.-Oct. 1973 in the lowlands (and July 1973 at high altitude). Larval hosts many plant families, but usually Compositae, including *Cirsium vulgare* (larvae raised to adults from near Salida), *Artemisia frigida, Anaphalis margaritacea* (many ovipositions elsewhere in Colorado for these two plants). *Vanessa* adults feed on various flowers of all colors, sometimes on sap (*atalanta*), or on mud.

V. atalanta (linn.) 36 loc: throughout the area, 4860-9800' (one record 11000'), on ridgetops and valley bottoms. Apparently two broods, the first from late June to early Aug., the second late Aug. overwintering to late May. Usually uncommon, but fairly common in 1973. Larval hosts Urticaceae, Moraceae, Ulmaceae.

V. carye annabella (Field). 9 loc: throughout the area including Pueblo and high altitude on both mountain ranges (probable Wet Mtn. Valley), 4860-13800'. Several broods, Aug. 6-Oct. 1 overwintering to late May at lower altitudes (perhaps a mid-summer brood has been missd), early July-Oct. 14 overwintering to mid June at higher altitudes. Rare. Larval hosts many Malvaceae; occasionally Urticaceae. We treat *V. annabella* as an allopatric North American subspecies of *carye*.

V. virginiensis (Drury) 18 loc: throughout the area (probable at high altitude in the Wet Mts.), 4300-13000'. There are apparently two broods at mid and higher altitudes, from late June to early Aug., and Aug. 23, Oct. 12, May 5 (apparently overwintering?). On the plains and foothills, records are June 12-28, July 12, and July 25-Aug. 14, perhaps indicating three broods (with an overwintering brood unsampled). Uncommon. Larval hosts Compositae; rarely Boraginaceae.

Euptoieta claudia (Cram.) 44 loc: throughout the area, 4300-12500' (a rare stray above 9000', up to 12000' on Greenhorn and Galena Peaks), usually in prairie habitats. Several broods mid May-Oct, with peaks in late May, mid June-early July, and late July on the plains, with few records after Aug. 3. Adults may migrate from lower altitudes and latitudes to higher ones. Common, especially at lower altitude and in certain years. Larval hosts Violaceae: *Viola*, sometimes *Linum*, *Sedum*, supposedly others. Adults often feed on flowers.

Speyeria aphrodite ethne Hemming. 54 loc: throughout the mountains and on the plains a few miles east of the foothills (one record 10 mi. W. Pueblo), 5200-9500' (rarely 10300'), in chaparral or open forests. One brood, June 24-Sept. 2 (extremes June 12-Sept. 13) main peak late June-late July). Adult females of some *Speyeria* seem to diapause; after diapause they may lay eggs in late summer. Diapause is most pronounced in *S. aphrodite*, *edwardsii*, and *coronis*, which have a very long flight perio. and females predominate at the end, although males of all three species occur as late as Aug. 24. In fact, there is a second peak of records in late August in all five local *Speyeria*. Also, dispersal seems to be greatest in the first three *Speyeria* listed and *S. mormonia* in late summer, when females are found on the plains, after diapause terminates. The two species with little or no diapause, *S. mormonia* and *atlantis*, occur in moister habitats. *S. aphrodite* is common. Larvae of all *Speyeria* feed on *Viola*. Adult *Speyeria* feed on flowers of many colors, and on mud.

S. edwardsii (Reak.) 32 loc: throughout the mountains and the plains a few miles east of the mountains (one record 11 mi. SSW Pueblo), 5200-12349' (usually 6000-9500'), mainly in shrubland or openings in forests. One brood, late June-Sept. 2 (extremes May 25-Sept. 13) (main peak late June). Common but less so than *S. aphrodite*.

S. coronis halcyone (Edw.) 33 loc: throughout the mountains (probable in Huerfano Park) and the plains a few miles east of the mountains (4 mi. E. of Canon City etc.), 6000-9500', mainly in open areas and chaparral. One brood, late June-Sept. 2 (extremes May 25-Sept. 13, main peak late June). Abundance similar to *S. edwardsii*.

S. atlantis hesperis (Edw.) 38 loc: throughout the mountains from 6600-10700', along streams, or in wet meadows (including the Arkansas Canyon bottom and Wet Mountain Valley bottom). One brood mid July-late Aug. (extremes June 21-Sept. 10, main peak late July). Common. In the Wet Mtn. foothills the unsilvered form ("*hesperis*") greatly predominates and occurs in drier habitats such as *Quercus* groves. Silvered forms ("*electa*" Edw.) are the majority in the rest of the area, especially in wet meadows. Along Medano Creek in the Sangre de Cristo mts., a wide variety of silvered and unsilvered forms occurs including very pale individuals approximating the pallid subspecies which occurs on Raton Mesa in New Mexico.

S. mormonia eurynome (Ewd.) 19 loc: Wet and Sangre de Cristo Mts., and mountains west of the San Luis Valley, from about 9800-13000', straying to lower altitudes late in the flight period to the San Luis Valley, Wet Mtn. Valley, Wet Mtn. foothills (7200'), and even to the plains near Denver. The usual habitat is subalpine meadows. One brood, late July-late Aug. (extremes July 13-Sept. 2). Common to abundant.

Boloria selene tollandensis (B. & B.) 4 loc: Wet Mtn. Valley floor, and in the San Luis Valley (west of Villa Grove), from 7600-8400', in wet meadows. On the plains north of this area several colonies of a subspecies with reddish brown VHW base occur; the plains here are too dry for the species. Apparently two broods in Wet Mtn. Valley, mid June-July 1, July 24-Sept. 7. In the plains subspecies peaks occur in early June, July, and late Aug.-early Sept. Populations at about 10,000' in the state are apparently only single brooded in late July. Common but very local. Larval foodplant *Viola* sp. (oviposition next to plants on drier mounds of a meadow near Westcliffe). Adult *Boloria* feed on flowers on various, often yellow, colors.

B. titania helena (Edw.) 10 loc: throughout the Sangre de Cristo Mts. (and Mt. Blanca) and Cochetopa Hills, absent from the Wet Mts., 10000-13000', in moist spots at the edge of bogs, and in swales above timberline. It is almost exclusively alpine in the Sangre de Cristo Mts. One brood, July 17-Aug. 5 (extremes June 29-Aug. 14). Common. Adults are associated with dwarf alpine *Salix*, which seems to be a larval food elsewhere, in Alberta (Ferguson 1954).

B. freija browni Higgins. 2 loc: upper Wet Mts. (north of Greenhorn Peak) and in the Cochetopa Hills (near Cochetopa Pass, also Marshall Pass), probable in the Sangre de Cristo Mts., from 10000-10500' (9500-12000' elsewhere in Colorado). It occurs in valley bottoms and at the edge of bogs where *Vaccinium* occurs. One brood, in June (extremes May 25-July 6). Common but very local. Larval foodplant *Vaccinium caespitosum* in Colorado. Adults feed on flowers (*Pulsatilla*, etc.) and mud.

Poladryas minuta arachne (Edw.) 64 loc: throughout the mountains in hilly areas, 6000-10500' (usually 6500-9300'). Adults occur almost continuously from May 28 to Sept. 6. Records are most frequent in late June, mid to late July, mid and late Aug. Because developmental period from egg to adult is about 7 weeks at 20°C, this may represent two broods for some individuals, fewer for others. Common. Larvae feed on *Penstemon* (Scott 1974b). Adults feed on flowers of all colors, mainly yellow ones.

Euphydryas chalcedona (= *anicia*). 22 loc: Wet Mts. from 6200-12349' (uncommon in the foothills, at Greenhorn and at Beulah), in the Sangre de Cristo Mts. from 9700-13800', and hills west of the San Luis Valley (Bonanza, 9600'; Nash 1893). *E. c. brucei* (Edw.) occurs above 11000' in both the Wet and Sangre de Cristo Mts., usually on tundra ridges. At middle elevations in the Wet Mts. (and Mosca Pass in Sangre de Cristo Mts.) an extremely variable population occurs (some individuals resemble subspecies *eurytion* (Mead), *capella* (Barnes) and *carmentis* (B. & B.) usually the former) in open grassland. Foothills specimens (not seen) may be *capella*. One brood, June-early July in foothills, June 30-Aug. 2 (extreme Aug. 16) at higher altitudes. Rare at low altitudes, common to abundant above 9000'. Larvae feed on various Scrophulariaceae including *Castilleja integra* (larvae raised to adults near Rosita). Adults feed on various flowers, often yellow or white ones. I have series from the Sierra Nevada of California and from Washoe County, Nevada in which individuals intergrade in genitalia and wing pattern between *chalcedona* and *anicia*, hence I provisionally unite these subspecies.

Chlosyne leanira fulvia (Edw.) 2 loc: plains, Wet Mtn. foothills, Arkansas Canyon (Box Canyon, Fleming Mtn.), and the Wet Mts. from Rosita to Greenhorn Peak, probable in Huerfano Park. The larval foodplant is locally abundant in the San Luis Valley but the insect apparently does not occur this far north in the Rio Grande drainage. 5000'-9300', once (a stray? male) 12349'. It is fairly widespread on the plains, usually on limestone ridges. It occurs at a gypsum quarry in the Arkansas Canyon. In the higher Wet Mts. it occurs on grassland ridges and hilltops near the larval host. The larval host, and therefore the butterfly, is highly restricted to calcareous soil. Three broods on the plains, May 3-June 5, June 26-July 26, Aug. 13-Sept. 6. One brood in the higher Wet Mts., July 6-26. Uncommon at higher altitudes, may be common or abundant on the plains. Larvae feed on *Castilleja integra* (Scott 1968; females lay egg clusters on lower leaves; larvae raised from Pueblo, Beulah, Wetmore). Adult *Chlosyne* feed on various flowers, often yellow ones, and on mud. Intergradation of adults and lack of major foodplant or larval differences suggest conspecificity of *leanira*, *alma*, and *fulvia*.

C. damoetas (Skin.) 6 loc: Sangre de Cristo Mts., 11400-13000', flying over rockslides near the larval host. One brood, July 9-Aug. 11. Fairly common but very local near the larval host, *Erigeron leiomeris* (a cluster of 63 eggs laid on leaf and adjacent rock at Hermit Pass). Adults feed on blue *E. leiomeris* and other flowers. Adults are slightly darker here than elsewhere in Colorado.

C. acastus (Edw.) 8 loc: Arkansas Canyon from near Nathrop to Wellsville (it may extend farther down the canyon) and around the San Luis Valley (Mosca to Rito Alto Creeks), possible in Huerfano Park. 7000-8500', mostly in gulch bottoms where *Chrysothamnus* is abundant. One brood, May 27-June 25. Uncommon. Larval hosts Compositae: *Chrysothamnus*, *Aster*. Adults have slightly heavier black markings than specimens from Utah.

C. gorgone (Hubn.) 28 loc: all over the plains, Wet Mtn. foothills, Arkansas Canyon, and Wet Mtn. Valley (south to Bull Domingo Hills). Probable in Huerfano Park, apparently absent in the San Luis Valley. 4300-8100', in chaparral, flats, etc. near larval hosts. About three broods on the plains, April 24-early June, late June-end of July, Aug. 8-Sept. 5. One brood elsewhere, mid May-early July (extremes May 5-July 14); larvae from these areas diapause half grown. Common. Larval hosts Compositae including *Helianthus pumilus* (larvae from Iron Dollar Gulch and Fleming Mtn., Fremont Co., raised to adults), *H. petiolaris* (larvae found in Hardscrabble Canyon), *H. annuus* (reared at Pueblo by Maurice Howard). Adults are associated only with *H. pumilus* at higher altitudes.

C. nycteis drusius (Edw.) 7 loc: plains (Pueblo, SE of Beulah), Wet Mtn. foothills (Rye to Hardscrabble Canyon) and northern Wet Mtn. Valley, possibly in San Luis Valley, 4800-7500', along streams. One brood, June 4-30 in the foothills (uncommon), late June-July 13 Wet Mtn. Valley (common). Larval host *Rudbeckia laciniata*; in Colorado it is always associated with *R. laciniata* along streams.

Phyciodes picta Edw. 16 loc: plains west to the mountains, and all along the Arkansas Canyon, probable in Huerfano Park, 4300-7100', on flat alkaline areas where *Convolvulus* is common especially along road and railroad tracks. About three broods, about May 11-mid June, early to late July, early Aug.-Sept. 8 (some individuals can be found all summer). Common. Larval hosts various *Aster* spp. (W. H. Edwards raised eggs obtained by Nash at Pueblo) and *C. arvensis.* Adult *Phyciodes* often feed on flowers, often yellow and white ones, and on mud.

P. campestris camillus Edw. 65 loc: throughout the area (including the Wet Mtn. and San Luis Valley floors and the plains east at least to Pueblo and farther east in Prowers County), 4800-9500' (rarely up to 10700'), more often in valley bottoms than elsewhere. Apparently four broods on the plains, May 4-June 8, June 13-early July, July 22-Aug. 12, Aug. 28-Sept. 13. Three broods elsewhere, end of May-start of July, mid July-early Aug., late Aug.-mid Sept. Common. Larval hosts *Aster,* including *A. ericoides* with which it is associated east of Colorado Springs. Edwards (1868-1897) raised larvae obtained from Nash at Pueblo on many *Aster* spp.

P. tharos (Drury) 45 loc: throughout the area (probable in Huerfano Park), 4300-9000', in moist valley bottoms, streamsides, and moist meadows. Apparently three broods on plains, early or mid May-early June, late June-early Aug., late Aug.-mid Sept. Mainly one brood Wet Mtn. foothills (May 25-Aug. 12, but most records late June-mid July). One brood in the Arkansas Canyon and higher altitudes, June 25-early Aug. Common. Larval hosts Compositae: *Aster, Verbesina.*

P. vesta (Edw.) Nash (1893) found strays of this Texas species at Doyle Ranch (SE of Pueblo), Hardscrabble Canyon, and Rosita. The larval foodplants (Acanthaceae) of *P. vesta* and *P. texana* are not native to Colorado.

P. texana (Edw.) One stray was caught near Coaldale in the Arkansas Canyon by Kathy Scott, June 27.

Cyllopsis pertepida dorothea (Nabokov). 34 loc: Wet Mtn. foothills, Arkansas Canyon as far upstream as Buena Vista, hills in Wet Mtn. Valley south to Bull Domingo Hills, Huerfano Park, and hills in San Luis Valley north to west of Villa Grove, 5800-9000', in gulches in the pinon-juniper or ponderosa pine belt. One brood, June 20-July 10 (rarely worn females to Sept. 2) in foothills, mainly mid July-mid Aug. elsewhere (range June 17-Sept. 10). Usually uncommon, sometimes common but very hard to catch in the underbrush and steep gulches. Larval hosts probably grasses. Adults almost never feed; one male fed at mud.

Coenonympha tullia ochracea Edw. 52 loc: throughout the area except the plains and San Luis Valley floor, 6300-10500', in grassland chaparral, open forests, etc. One brood May 21-July 6 in Wet Mtn. foothills, May 27-late July (peak late June) elsewhere. Common. Larvae feed on various grasses in the laboratory, and on sedges in Europe. Adults often feed on flowers, especially yellowish or whitish ones.

Cercyonis pegala boopis (Behr) 45 loc: plains, Wet Mtn. foothills, Arkansas Canyon, Wet Mtn. Valley south to Lake Creek, probable in Huerfano Park but absent in San Luis Valley, 4300-8100', often in valley bottoms, frequent in cottonwood groves on the plains. One brood, June 27-mid Aug. in the plains and foothills (peak late July, females as late as Sept. 13), July 1-late Aug. (peak end of July, extreme Sept. 10) in the Arkansas Canyon. Common. Larvae feed on various grasses. Occasional females have slightly yellowish patches on the dorsal forewing, especially on the plains. Adults feed on willow and poplar sap and often on flowers (especially bluish ones) including *Tamarix, Solidago, Medicago, Cirsium,* and on mud.

Neominois ridingsii (Edw.) 34 loc: throughout the area, except only one record in Wet Mtn. foothills (NE of Oak Creek Camp) and only one record on plains (east of Greenhorn just east of the foothills), although it extends east of the Front Range to Cheyenne County. 6100-13000' (usually below 10000', but occurs above this at Hayden, Hermit (two dates, 13000'), and Music Passes). It occurs in grassland, sometimes in pinyon-juniper woodland. One brood, early June-July 4 on the plains, mid-June-late July elsewhere (extremes June 9-Aug. 16) (peak late June near Salida, early July in San Luis Valley). Common. Larvae feed on grasses in the lab (Edwards, 1868-1897), oviposit on *Bouteloua gracilis* and other plants (Bear Creek, Chaffee Co.; Scott 1973a). Adults rarely feed, on various (mainly yellow) flowers.

Oeneis chryxus (Dbdy.) 28 loc: Wet Mts. (only two records in the foothills at Beulah and between North Creek and South Hardscrabble Creek, but widespread from 9000-12349' west to Rosita and Devil's Holein Huerfano Park) and Sangre de Cristo Mts. (above 9000' on the east side, above 8500' on the west side), and the hills on the west side of the San Luis Valley (southwest of Villa Grove, Bonanza). Mostly in grassy areas especially on ridges, 7000-13000', most widespread above timberline, local below. One brood, May 25-July 28 below 10000' (peak late June), July 1-31 above. Uncommon to common. Larvae undoubtedly feed on unknown monocotyledons. Adult *Oeneis* seldom feed; *O. chryxus* was observed feeding on a yellow composite and on mud. This species probably has a two year life cycle because we

C. oetus charon (Edw.) 57 loc: throughout the area except for the plains and the floor of the San Luis Valley, 6300-10300', in grassland, chaparral, or open forest. One brood, June 28-Aug. 2 (peak mid July) in the foothills, July 9-Sept. 10 (peak late July) elsewhere. Common. Larvae from Rosita and Salida were raised on grasses by W. H. Edwards (1868-1897). Adults feed on many flowers of al

C. meadii alamosa Emmel & Emmel. 14 loc: San Luis Valley, on the valley floor and hills at the edge (*C. oetus* occurs at the edge and at higher elevations in the San Luis Valley), 7500-8600', in grassland, chaparral, or open woodland. It is common in El Paso County even on the plains 10 mi. east of Colorado Springs, southwest to Phantom Canyon, but is absent in our area except for the San Luis Valley. One brood, July 18-Aug. 22 (peak early Aug.). Common. Larval foodplants are grasses; it is often associated with *Bouteloua gracilis*. Adults feed on flowers of various colors. Adults have a slightly more pronounced ventral hindwing band here than northward.

have 36 records during even-numbered years but only 3 records for odd-numbered years.

O. alberta oslari Skin. 3 loc: north side of the Arkansas Canyon (Echo Canyon, 8700'), the Cochetopa Hills west of the San Luis Valley (10000-10500'); also south of the area on Raton Mesa (9000'). Many promising habitats in the Wet and Sangre de Cristro Mts. were searched without success. One brood, mid May-early June (range May 3-June 24), in bunch-grassland. Usually common but very local. Larvae feed on monocotyledons, reportedly on *Festuca*. Adults from Cochetopa Hills are grayer than those elsewhere. Many adults fed on mud by landing on the downwind side of a pond then flapping and crawling toward the mud.

O. uhleri (Reak). 13 loc: Wet Mts. (Rosita (Nash), north and NW of Greenhorn Peak), Sangre de Cristo Mts. (only in the Rio Grande side except on Poncha and La Veta Passes) and the Cochetopa Hills, 8900-10500', in bunch-grass habitats. One brood, early June-early July (range May 27-July 17). Common but local. Larvae probably feed on bunch grasses. Adults feed on mud and rarely on flowers.

O. melissa lucilla B. & McD. 4 loc: Sangre de Cristo Mts. (so far only south of Hayden Pass southward to Mt. Blanca). 12000-13800', on alpine ridges. One brood, July 2-Aug. 1. Often common. Larvae feed on monocotyledons, including *Carex*.

Erebia magdalena Strecker 8 loc: Sangre de Cristo Mts. on Mt. Blanca and north and south of Hayden Pass, 11600-13800', flying over rockslides. One brood, July 3-Aug. 5. Uncommon, occasionally common. Larvae undoubtedly feed on monocotyledons, including *Carex* (oviposition observed by J. Emmel, pers. comm.), and eat *Poa pratensis* in the lab (reared by Michael Young).

O. alberta oslari Skin. 3 loc: north side of the Arkansas Canyon (Echo Canon, 8700'), the Cochetopa Hills west of the San Luis Valley (10000-10500'); also south of the area on Raton Mesa (9000'). Many promising habitats in the Wet and Sangre de Cristo Mts. were searched without success. One brood, mid May-early June (range May 3-June 24), in bunch-grassland. Usually common but very local. Larvae feed on monocotyledons, reportedly on *Festuca*. Adults from Cochetopa Hills are grayer than those elsewhere. Many adults fed on mud by landing on the downwind side of a pond then flapping and crawling toward the mud.

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O. melissa lucilla B. & McD. 4 loc: Sangre de Cristo Mts. (so far only south of Hayden Pass southward to Mt. Blanca). 12000-13800', on alpine ridges. One brood, July 2-Aug. 1. Often common. Larvae feed on monocotyledons, including *Carex*.

Erebia magdalena Stiecker 8 loc: Sangre de Cristo Mts. on Mt. Blanca and north and south of Hayden Pass, 11600-13800', flying over rockslides. One brood, July 3-Aug. 5. Uncommon, occasionally common. Larvae undoubtedly feed on monocotyledons, including *Carex* (oviposition observed by J. Emmel, pers. comm.), and eat *Poa pratensis* in the lab (reared by Michael Young).

E. epipsodea Butt. 12 loc: Sangre de Cristo Mts. (at least south of Hayden Pass to La Veta Pass), and mountains west of the San Luis Valley (Bonanza, Cochetopa Hills), absent from the Wet Mts., 9200-13000', in moist meadows and swales. Most records in this area are above timberline, contrasting with the Front Range where some colonies occur in the foothills as low as 6800' (in late May-mid June). One brood, June 17-July 19 below timberline, July 16-Aug. 1 (extreme Aug. 23) above timberline. Common. Larvae feed on various grasses and sedges. Adults rarely feed on flowers (white *Saxifraga* etc.), sometimes feed on mud.

Libytheidae

Libythea bachmanii larvata (Strecker) Two strays from farther south were caught near Pueblo by Maurice Howard, Aug. 9 and Sept. 2, one San Luis Valley So. of Moffat (J. Brock, Aug. 8).

Lycaenidae

Apodemia mormo near *mejicanus* (Behr) 33 loc: throughout the area including the plains north of Pueblo and the Wet Mtn. and San Luis Valley floors, 5000-9000', in grassland, chaparral, and pinon-juniper woodland etc., always on or near *Eriogonum jamesi*. One brood, about Aug. 1-26 on the plains, July 21-Aug. 26 in the Arkansas Canyon and Wet Mtn. Valley, July 17-mid Aug. in the San Luis Valley (extremes July 1-Aug. 30). Uncommon to common. Larval host *Eriogonum jamesi* (several ovipositions observed near Colorado Springs and one east of Buena Vista). Adults feed on *E. jamesi*, sometimes on various other (mainly yellow) flowers. Adults have slightly less red than those from farther south in New Mexico and Texas. Plains individuals are larger than those from the mountains.

A. nais (Edw.) 13 loc: Wet Mtn. foothills, Huerfano Park. the west edge of the Wet Mtn. Valley, the Arkansas Canyon (so far only 12 miles north of Salida to Buena Vista), and the hills bordering the San Luis Valley, 6800-9200', near *Ceanothus fendleri*. One brood, June 22-July 28 in the foothills, early July-Aug. 1 elsewhere. Uncommon. Larval host *Ceanothus fendleri* (Rhamnaceae; ovipositions on leaves next to inflorescence and on a lower branch in Hardscrabble Canyon, Fremont Co.; I reared it on *C. fendleri* elsewhere in Colorado). Adults feed on *C. fendleri, Apocynum* (both whitish) and on mud. Strangely, Kendall (1976, for *nais chisosensis*), and Edwards (1868-1897, for *nais nais* from Arizona) give *Prunus* as the larval host.

Hypaurotis crysalus (Edw.) 28 loc: throughout the mountains and plains next to the mountains (south of the Arkansas River to Bull Domingo Hills, and north to Hayden Pass in San Luis Valley drainage, 5850-8700', on *Quercus gambellii*. One brood, June 29-mid Aug. (extreme Aug. 2) in the foothills, July 13-Aug. 28 elsewhere. Usually common, sometimes very abundant. Larval host *Q. gambellii* (ovipositions Lake Creek Campground, Custer Co., Scott 1974e). Adults feed on oak sap, raindrops, and occasionally on mud, never on flowers.

Strymon melinus franki Field. 44 loc: throughout the area, but rare in the Wet Mountain Valley (Rosita, etc.) and San Luis Valley (west of La Veta Pass, Great Sand Dunes), 4300-9000' (usually below 7300'). Perhaps four broods on the plains, April 18-May 21, mid June-July 11, July 22-Aug. 17, late Aug.-Oct. In the Arkansas Canyon records are June 9-July 1, many from July 5-30, and scattered records to Sept. 15. In the Wet Mtn. and San Luis Valleys records are July 3-Aug. 12. Uncommon. Larvae feed on reproductive parts, rarely leaves, of a very wide variety of plants. Adult Theclini, a tribe including *Hypaurotis* to *Callophrys*, feed on many flowers of all colors but primarily of yellow or whitish colors (*Hypaurotis*, *Satyrium acadica* and *sylvinus* seem to be exceptions); the difference in flowers preferred by Theclini and Hesperiinae is often noticeable in the field (Scott 1974a). Adults also feed on mud.

Harkenclenus titus (Fabr.) 25 loc: throughout the area except the flat San Luis Valley and Wet Mtn. Valley floors (probable in Huerfano Park) from 4300-9000', near *Prunus virginiana*. One brood, June 24-Aug. 3 on the plains, July 15-mid Aug. (extreme Aug. 27) above 8000'. Uncommon, occasionally common, once by the hundreds on a pure stand of *P. virginiana* plants on the Great Sand Dunes. Larval hosts various *Prunus* (Rosaceae), supposedly on *Quercus* and *Eupatorium*.

Satyrium calanus godarti (Field) 46 loc: throughout the area including the plains next to the mountains (north in San Luis Valley to Ferguson Creek, south in Wet Mountain Valley to Bull Domingo Hills). 5850-8800', on or near *Q. gambellii*. One female from Junkins Park Creek, 9200', in the Wet Mts. was found far from *Quercus gambellii*. One brood, June 22-Aug. 2 (peak early July) foothills, July 1-Aug. 24 (peak late July) elsewhere. Common. Larval hosts *Q. gambellii* (*Fraxinus* etc. elsewhere).

S. liparops aliparops (Mich. & Dosp.) 8 loc: Wet Mtn. foothills, the Arkansas Canyon, and the northern Wet Mtn. Valley (Lake Creek), 6600-8200', mostly in gulches near or in groves of *Quercus gambellii* and *Prunus virginiana*. One brood, end of June-Aug. 2 in the foothills, July 10-Aug. 7 elsewhere. Rare-uncommon. Larval hosts are various trees and shrubs including *Prunus virginiana, Quercus, Crataegus*. A published record of *Acer negundo* (Scott et al. 1968) is erroneous.

S. behrii crossi (Field) 27 loc: throughout the mountains, south in the Wet Mtn. Valley to Rosita, north to west of Villa Grove in the San Luis Valley, 6400-8800', near *Cercocarpus montanus*. One brood, June 25-July 25 foothills (peak start of July), July 1-Aug. 3 (extreme June 21, peak mid July) elsewhere. Fairly common. Larval host *Cercocarpus montanus* (associated with in the Pueblo area, ovipositions seen north of the area).

S. sylvinus (Bois.) *ssp.* 16 loc: Wet Mtn. foothills, the adjacent plains (east of Rye, east of Florence, Canon City), all along the Arkansas Canyon, the Wet Mtn. Valley south nearly to Hillside (rare), and the SanLuis Valley floor. Probable in Huerfano Park. 5150-7750', on or near *Salix exigua*. One brood, July 7-Aug. 3 foothills and plains, July 10-Aug. 14 elsewhere. Uncommon to common. Larval host *S. exigua* (oviposition Mirage, Saguache Co.) Adults feed on *Asclepias, Cirsium*, etc.

S. acadica (Edw.) *ssp.* 2 loc: plains (Pueblo and Canon City), 4800-5300', on or near *Salix exigua*. One brood, July 5-Aug. 2. Uncommon to common but local. Larval host *S. exigua* (oviposition Canon City). Adults feed on *Asclepias, Medicago, Melilotus, etc. S. acadica* and *S. sylvinus* fly in the same willow clump in Canon City.

Callophrys nelsoni siva (Edw.) 39 loc: throughout the mountains, the plains east to Pueblo, south in the Wet Mtn. Valley to Round Mountain, north in the San Luis Valley to near Villa Grove, 4800-8800', on or near juniper trees. One brood, late April-Aug. 1 foothills (peak early June, worn after late June), May 27-July 25 elsewhere (peak late June). Common. Larvae feed on various *Juniperus* spp. I treat *siva, loki, barryi, byrnei*, and *rosneri* as allopatric subspecies of *nelsoni* pending proper studies. They tend to intergrade (*loki-siva* populations exist, and the violet ventral color of *nelsoni* occurs in western *siva* populations), and foodplant differences are not clearcut (*nelsoni* occurs on *Juniperus occidentalis*, for instance). John Lane is conducting foodplant studies.

C. spinetorum (Hew). 8 loc: Wet Mtn. foothills, Arkansas Canyon (one record NE of Salida), and mountains surrounding the San Luis Valley. Probable in hills in Huerfano Park and in Wet Mtn. Valley. 6200-9000', in pine forests. One brood, May 1-June 29 foothills, May 28-July 16 (peak late June) at higher elevations. Rare; uncommon around Beulah. Larvae feed on *Arceuthobium* parasitic on many conifers.

C. eryphon (Bois.) 30 loc: throughout the mountains, including the plains-foothills ecotone (north of Goodpasture, etc.), south in Wet Mtn. Valley drainage to Rosita, north in San Luis Valley drainage to Wild Cherry Creek and Luders Creek Camp. Probable Huerfano Park. 6000-9200' (rarely 10000'), in pine forests. One brood, April 24-July 5 (peak late May in foothills), May 26-July 1 elsewhere. Common. Larvae feed on needles (Hardy 1959) and on male cones (Newcomer 1973) of pines; associated with *Pinus ponderosa* and *P. edulis* here.

C. polios obscurus Ferris & Fisher 12 loc: Wet Mts., the west edge of the Wet Mtn. Valley, and the Cochetopa Hills. Probable at proper elevations in other mountains in the area. 7500-10000', on or near *Arctostaphylos uva-ursi* in forests. One brood, April 27-June 4 at lower elevations in Wet Mts., May 3-June 20 elsewhere. Common. Larval host *A. uva-ursi*. Adults feed mainly on *A. uva-ursi* flowers.

C. augustinus iroides (Bois.) 7 loc: Wet Mts., both sides of the Wet Mtn. Valley, and the Cochetopa Hills. Probable in other mountain areas. 8000-10000', on or near *A. uva-ursi*. One brood, May 2-29 in lower Wet Mts., mid May-mid June elsewhere. Uncommon. *A. uva-ursi* is undoubtedly the main or only larval host here. Adults feed on *A. uva-ursi* flowers.

C. mossii (H. Edw.) *ssp.* 4 loc: Wet Mtn. foothills (Oak Creek Canyon vicinity; Don K Ranch) and Phantom Canyon NE of Canon City, 6400-7500', males in canyon bottoms and females on north-facing hillsides near *Sedum lanceolatum*. One sight record just west of Buena Vista, Chaffee Co., may be this species. One brood, April 19-late May. Uncommon. Larvae feed on *S. lanceolatum*. Adults have a more straight ventral hindwing postmedian line here than in the Front Range.

C. dumetorum homoperplexa B & B. 33 loc: everywhere in the mountains and on the Wet Mtn. Valley floor around Westcliffe, from 6400-9200', in chaparral, open woodland, grassland, etc. One brood, April 18-July 10 foothills, May 30-Aug. 4 elsewhere. Common. Larval hosts *Eriogonum*, associated usually with *E. jamesi* and rarely with *E. umbellatum* in the Pueblo area. One oviposition on *Ceanothus fendleri* (Scott et al. 1968) was apparently accidental, as this plant does not occur in some sites. Since my revision of *Callophrys* in Howe (1975) I now think that *C. dumetorum, affinis*, and *apama* are intergrading subspecies of each other. *C. d. washingtonia* represents an intergrade population between *C. d. dumetorum* and *C. d. affinis*, and *C. d. affinis* intergrades with *C. d. apama* in southern Utah.

Lycaena cupreus snowi (Edw.) 2 loc: Sangre de Cristo Mts. (West Creek Lake, Hermit Pass), 11500-13000', in glacial cirques and other moist hollows where snow lingers, near *Oxyria digyna*. One brood, July 3-Aug. 11. Uncommon. Larvae feed on *Oxyria digyna* (oviposition on rock next to *O. digyna* at Hermit Pass, Custer Co.). Adults feed on various (mostly yellow) flowers.

L. rubidus sirius (Edw.) 49 loc: throughout the area including the plains east of Pueblo and the Wet Mtn. and San Luis Valley floors, 4600-9800', along streams near *Rumex*. One brood, June 15-Aug. 2 plains and foothills, July 8-Aug. 25 (once June 24) in Arkansas Canyon and San Luis Valley, July 15-Sept. 1 Wet Mtn. Valley. Common. Larval hosts *Rumex*, including *R. salicifolius triangulivalvis, R. densiflorus, R. crispus, R. occidentalis*; associated with the last three *Rumex* and with *R. utahensis* at various locations in the Pueblo area. Adult *Lycaena* feed occasionally on mud, often on flowers especially yellowish (sometimes whitish) ones. Females in this area are almost all red dorsally, as are those from the plains in Denver north of this area.

L. heteronea gravenotata Klots. 19 loc: Arkansas Canyon, Wet Mtn. Valley floor and hills, Huerfano Park, and San Luis Valley except the floor (present in foothills of the Front Range but not in foothills in the Pueblo area), 6800-9000', in prairie and woodland near *Eriogonum jamesi*. One brood, July 18-Aug. 24, slightly earlier in the San Luis Valley. Usually uncommon. The major larval host is *E. jamesi* (oviposition SW of Trout Creek Pass, Chaffee Co.), others are *E. umbellatum* and *E. subalpinum*. All specimens in the Pueblo area are the heavily spotted subspecies *gravenotata*.

L. helloides (Bois.) 34 loc: 1) Ecotype A: the plains, Huerfano Park, Wet Mtn. foothills (rare, near Beulah and Hardscrabble Canyon), and Wet Mtn. and San Luis Valley floors including Rosita (4300-9000', several broods); 2) Ecotype B: the higher Wet and Sangre de Cristo

Mts. including west of the Arkansas Canyon (the species is absent in the canyon bottom), and the mountains surrounding San Luis Valley (Bonanza on the west side) (9000'-11000' except 8000' at Hayden Creek Campground, one brood). Meadows, along streams and ditches, always near *Rumex* or *Polygonum*. Three broods on the plains, May 10-June 14, July 10-early Aug., Aug. 27-Oct. 15. Perhaps three broods in the Wet Mtn. Valley and San Luis Valley, June-mid July, late July-mid Aug., Aug. 18-early Sept. One brood in the higher mountains, July 11-Aug. 25. Common. Larval hosts Polygonaceae in Colorado including *Rumex salicifolius triangulivalvis*, *R. acetosella*, *R. densiflorus*, *Polygonum aviculare*, *P. douglasii*; in the Pueblo area associated with *Rumex crispus* and *Polygonum pennsylvanicum* at low elevations, with *R. densiflorus* and *R. occidentalis* at higher altitudes. Adults feed on many flowers including *Asclepias*, *Achillea*, *Erigeron*, *Potentilla*. J. Scott (in press) shows using extensive foodplant and morphological data that all Colorado material formerly referred to as *helloides*, *dorcas*, and *dorcas florus*, is *helloides*. High altitude material is somewhat darker than at low altitude but much individual variation occurs; the one-brooded "ecotype" in this area is only slightly darker than the several-brooded one. The lightest population in Colorado is on the floor of the San Luis Valley.

L. hyllus (Cram.) 6 loc: plains and Wet Mtn. Valley bottom (a distribution nearly identical to the several-brooded *L. helloides* ecotype), 4300-8000', in meadows and streamsides near *Rumex*. Two broods on the plains, June 15-July 20, Aug. 13-Sept. 10 (extremes June 10-Oct. 2). Apparently one brood in Wet Mtn. Valley, July 21-Aug. 23. Uncommon to common. Larval hosts *Rumex crispus* and *Polygonum coccineum* in Colorado; associated with *R. crispus* and *Polygonum pennsylvanicum* near Canon City. Adults feed on *Asclepias* and other flowers.

L. xanthoides dione Scud. 2 loc: plains (Canon City, Avondale), 4300-5400', in meadows and streamsides near *Rumex*. One brood, June 20-July 26 (extreme June 6). Uncommon to common. Larval hosts *Rumex* (Scott & Opler 1974) including *R. salicifolius triangulivalvis*, *R. crispus*, *R. occidentalis*; associated with *R. crispus* at Canon City. Adults feed on *Asclepias*, and other mostly yellow flowers.

L. arota schellbachi Tilden 44 loc: throughout the mountains including the plains next to the mountains (Crow, etc.), south in the Wet Mtn. Valley drainage to Bull Domingo Hills, north in San Luis Valley drainage to west of Villa Grove. 5900-9000', usually in canyon bottoms near *Ribes*. One brood, July 10-about Aug. 20 (extremes July 1-Sept.

14), peak late July everywhere. Common, sometimes abundant. Larval hosts *Ribes* (Scott 1974d) including *R. leptanthum* (ovipositions Spring Creek, Fremont Co.). Adults feed on many (mostly yellow) flowers, on *Rubus* berries, occasionally on mud.

Plebejus melissa melissa (Edw.) 76 loc: throughout the area, 4300-10600' (usually under 9000'), mostly in grassland habitats. Apparently four broods on plains, May 4-June 4, June 13-July 13, July 19-Aug. 16, Aug. 24-Sept. 13 (one record Oct. 22). Two, perhaps three broods at higher elevations, May 26-July 13, July 18-Sept. 10 (peaks in late June, late July, late Aug.). Common. Larval hosts many legumes, including *Astragalus bisulcatus* (larvae raised by W. H. Edwards from Pueblo), *A. miser* (15 ovipositions mainly on stems, 2 mi. E. of Alamosa, Alamosa Co.), *Oxytropis sericea* (4 eggs on lower stems, NW of Gardner, Huerfano Co.). Adult Plebejini feed on many flowers, and seem to prefer yellow slightly more than blue or red-blue ones. They often feed at mud, and sometimes (*Everes, Celastrina*) congregate there.

P. acmon lutzi dosp. 35 loc:throughout the area, 4300-12500' (usually below 9000', but apparently breeding above timberline in the Sangre de Cristos at Dry Lakes, Hermit Pass, Baldy Peak), mostly in grassland habitats on *Eriogonum*. Three broods on the plains, May 4-June 8, June 26-July 31, Aug. 18-Sept. 14. One brood above timberline, July 16-29. Two broods at middle elevations, June 12-July 10, July 18-Aug. 28. Common. Larval hosts *Eriogonum effusum* (ovipositions on pedicels at Westcliffe; the main or sole host below timberline), associated with *E. flavum* above timberline on Baldy Peak, with *E. cernuum* at Kerr Gulch. The dorsal hindwing orange border is narrower at high altitude. San Luis Valley individuals more closely resemble the ssp. *texanus* Goodpasture than ssp. *lutzi* (Goodpasture, 1973).

P. saepiolus whitmeri Brown. 57 loc: throughout the mountains and mountain valleys (not in the arid San Luis Valley floor or in the lower foothills, and in the Arkansas Canyon only in side canyons), 7000-12850', in meadows and streamsides near *Trifolium*. One brood, June 4-July 26 (peak end of June) in the lower Wet Mts., July 3-Aug. 11 near timberline, June 14-Aug. 28 (peak about July 10) elsewhere. Common, especially near timberline, but uncommon at the lowest elevations (a colony occurs on the plains in Boulder County east of the Front Range). Larval hosts many *Trifolium*.

P. icarioides lycea (Edw.) 38 loc: throughout the mountains (absent in the lower foothills, absent Arkansas Canyon bottom except in side

canyons such as Hayden Creek), 7000-10500′, near *Lupinus argenteus*. One brood, June 14-Aug. 16 (few upper foothills records, apparently early June-mid July). At high elevations in Clear Creek and Eagle Counties females are largely blue; this phenotype occurs as far south as Pine Creek in Chaffee County. On the plains just north of this area an ecotype similar in appearance to the main ecotype, associated with late-blooming *L. argenteus*, flies from Aug. 5-Sept. 9. Common. Larval hosts *Lupinus*, mainly or entirely *L. argenteus* in the Pueblo area.

P. icarioides lycea (Edw.) 38 loc: throughout the mountains (absent in the lower foothills, absent Arkansas Canyon bottom except in side canyons such as Hayden Creek), 7000-10500', near *Lupinus argenteus*. One brood, June 14-Aug. 16 (few upper foothills records, apparently early June-mid July). At high elevations in Clear Creek and Eagle Counties females are largely blue; this phenotype occurs as far south as Pine Creek in Chaffee County. On the plains just north of this area an ecotype similar in appearance to the main ecotype, associated with late-blooming *L. argenteus*, flies from Aug. 5-Sept. 9. Common. Larval hosts *Lupinus*, mainly or entirely *L. argenteus* in the Pueblo area.

P. shasta pitkinensis F.8 loc: Wet (Greenhorn Peak) and Sangre de Cristo Mts. (north and south and including Hayden Pass), 10700-13000', on cushion plant community on partly bare ground on subalpine or alpine slopes and ridgetops. One brood, July 13-Aug. 16. Common. Larval hosts legumes including *Trifolium dasyphyllum* (ovipositions Baldy Peak). There is some geographic variation in male color: Hermit Pass, gray-blue; Baldy Peak, West Creek, and Hayden Pass, more azure blue, especially the latter; Greenhorn Peak, more sky-blue; Loveland Pass and San Juan Mountains, smaller, more violet blue; Moffat County, violet blue, wider dark dorsal border. Weak movement has apparently allowed local phenotypes to evolve.

Plebejus glandon rustica (Edw.) 57 loc: almost everywhere in the mountains, 6800-13600', in high prairie (Westcliffe), pinon-juniper (Arkansas Canyon and in the San Luis Valley SW of Villa Grove), and alpine tundra. One brood, at least June 17-July 10 foothills (peak late June), July 5-Aug. 16 above 10000', May 26-Aug. 28 (mainly late June through July) elsewhere. Common. Larval hosts Primulaceae: *Androsace septentrionalis* (oviposition and 26 eggs found, 21 on underside of leaves, 1 on upperside, 4 on calyx, NE of Salida) at low altitudes, *A. carinata* (ovipositions at Hermit Pass) above timberline. *Plebejus* is the genus *glandon* is now placed in (J. Downey, in Howe

1975). I use *glandon* rather than *aquilo* for the species' name because Colorado material resembles European *glandon* rather than *aquilo,* Colorado foodplants are Primulaceae like European *glandon* rather than *Astragalus,* the foodplant of European and North American *aquilo,* and because *glandon* was named before *aquilo* (in case these two are conspecific).

Euphilotes battoides centralis (B. & McD.) 40 loc: throughout the area including the plains near Pueblo (and east to Baca County), the Wet Mtn. Valley floor and hills south to Rosita, the San Luis Valley hills north to west of Villa Grove, 5000-9000', always on or near *Eriogonum jamesi* in grassland or open woodland. One brood, August on the plains, June 16-Aug. 20 (mostly July 10-Aug. 6) elsewhere. Uncommon, common in some years. Larval host *Eriogonum jamesi* throughout this area.

E. rita coloradensis (Mattoni) 10 loc: Wet Mtn. Valley bottom from just south of Westcliffe north to the Arkansas Canyon; Arkansas Canyon from Texas Creek to Chalk Creek, and hills in the San Luis Valley (west of Villa Grove, Great Sand Dunes), probable in Huerfano Park. It occurs on the plains east of Colorado Springs but not in the lower hotter areas here and near Denver although *Eriogonum effusum* is common on these plains. 6300-8200', in grassland or pinon-juniper woodland on *E. effusum* (growing on pure sawdust at one site). One brood, July 18-Aug. 25 (so far July 18-22 in San Luis Valley), later northeast of the area on the plains. Uncommon, abundant in some years. Larval host *E. effusum* (ovipositions on flowers at Westcliffe).

E. spaldingi. (B. & McD.) 3 loc: mountains on the west side of the San Luis Valley just south of the Rio Grande, 8500-8900', in open pine woodland, June 30-Aug. 5. Uncommon, abundant in some years. Larval host *Eriogonum racemosum*; adults feed on *E. jamesi* and other flowers and on mud. The ventral hindwing red band is as wide as on ventral forewing, whereas in Utah it is narrower.

Everes amyntula (Bois.) ssp 34 loc: throughout the mountains including the plains-foothills ecotone, 6000-9400', in chaparral or oak woodland mostly in valley bottoms. Apparently two or three broods in the foothills, April 28-June 4, June 12-July 7 (perhaps one long brood but records peak in mid May and late June), July 26-Aug. 3 (much less common, perhaps a partial brood); two broods elsewhere, June 10-mid July, mid-July-Aug. 27 (the second brood perhaps partial). Common in spring, less common later. Larval hosts various legumes; associated with *Astragalus miser* at Lake Creek Campground, Custer Co.

E. comyntas (Godart) 4 loc: plains and lower foothills, sympatric with *E. amyntula* in Hardscrabble Canyon, 4300-7000', in meadows and streamsides near *Trifolium repens*. Apparently three broods, mid May-early June, late July, Aug. 16-Sept. 13, and some records between these three periods. Uncommon early in the year but common in late summer. Larval hosts legumes including *Trifolium repens* (ovipositions on and between flowers east of Colorado Springs, El Paso Co.). Adults feed on *T. repens* and other flowers. Records for *comyntas* and *amyntula* are based on genitalic identification.

Glaucopsyche lygdamus oro Scud. 46 loc: almost everywhere in the mountains, and the plains a few miles east of the mountains, including meadows SW of Westcliffe in the Wet Mtn. Valley and north of Villa Grove in the San Luis Valley, 5800-10600', in grassland, woodland, etc. One brood, April 14-July 2 in plains-foothills, May 24-July 19 elsewhere. Common. Larval hosts many legumes including *Astragalus miser* (12 eggs on flower buds, 11 on immature leaves, 8 on mature leaves at Saguache Park in Cochetopa Hills, associated with *A. miser* on La Veta Pass).

G. piasus daunia (Edw.) 11 loc: throughout the mountains, including the Wet Mountain Valley floor south of Westcliffe, probable in valleys flowing into the Arkansas Canyon, so far only in Conejos Co. in the San Luis Valley drainage. 7000-9200', near *Lupinus argenteus*. One brood, May 20-July 4 foothills, June 1-July 19 elsewhere. Rare to uncommon. Larval hosts *Lupinus argenteus* in Colorado; also reported on *Astragalus*.

Celastrina argiolus cinerea (Edw.) 22 loc: throughout the mountains including the plains within a few miles of the mountains, probable in Huerfano Park, along the Arkansas Canyon so far only west of Buena Vista, 6000-11000', mostly along streams and valley bottoms. One brood, April 24-June 28 foothills, May 24-July 15 elsewhere. Uncommon. Larvae feed on buds and flowers of very many plants including *Jamesia americana* and *Humulus lupulus* in Colorado. All the specimens from the Pueblo area are form *violacea*; other Colorado forms do not occur. Forms *lucia* and *marginata* are abundant on the western slope of the continental divide south to Archuleta County Colorado, but are rare in the Front Range of Colorado. Form *pseudargiolus* (a late May white form) occurs west of Denver in the Front Range. Form *neglecta* is rare in Colorado (I caught one just north of the Pueblo area in El Paso Co., Aug. 8, and Marc Epstein caught another in Boulder Co. in Aug.).

Brephidium exilus (Bois.) 8 loc: plains, Huerfano Park, lower foothills

(Phantom Canyon). 1 specimen from the Wet Mtn. Valley floor NW of Westcliffe (7800', July 9) may have bred there; if so, the species probably occurs in the Arkansas Canyon. 4500-6900', near larval hosts mostly on alkaline flats. Perhaps five broods, May 5, June 14, July 15-Aug. 3, Aug. 14-Sept. 14, Sept. 30-Oct. 22. Uncommon, most common in late summer when it is occasionally abundant on the plains. Larval hosts Chenopodiaceae, mainly *Atriplex*. Adults sometimes feed (once seen on *Melilotus alba* flower).

Hemiargus isola alce (Edw.) 51 loc: throughout the area, 4300-12483' (only 5 records above 9200', including north of Greenhorn Peak, and 12483' on Galena Peak). About four broods plains-foothills, May 11-June 3, June 24-early Aug., mid Aug.-Sept. 6, late Sept.-Oct. 22. About two or three broods elsewhere, June 3-July 3, July 11-Aug. 28 (Oct. 25 in San Luis Valley). Common at low elevations in some years, especially along steams near *Trifolium repens*. Larval hosts legumes including *T. repens* (ovipositions on flowers at Wetmore).

Leptotes marina (Reak.) 13 loc: plains, Arkansas Canyon, northern Wet Mtn. Valley (west of Hillside), and San Luis Valley (Rito Alto Creek), probable Huerfano Park. The species is migratory, but may overwinter occasionally. 4300-8500', most frequent on the plains in irrigated or streamside habitats. Almost continuous records from May 22-Oct. 22 suggest perhaps four broods. Uncommon, most common in late summer. Larval hosts legumes.

Hesperiidae

Epargyreus clarus (Cram.) 12 loc: plains, all along the Arkansas Canyon, Huerfano Park, and the San Luis Valley drainage (La Veta Pass), probable in Wet Mtn. foothills. 4300-7000' in most of Colorado, but in Huerfano Park and Las Animas County it often occurs up to 11600'. Usually in valley bottoms. One brood, mid June-mid July (extremes May 27-Aug. 1, usually July at higher elevations. Uncommon. Larval hosts legumes including *Robinia neomexicana* and *Glycyrrhiza lepidota* in Colorado. Adult Pyrginae very often feed on flowers of all colors, often bluish ones, and on mud (more specific data are given below for some uncommon species).

Thorybes pylades (Scud.) 16 loc: Wet Mtn. foothills and plains-foothills ecotone, Arkansas Canyon (Hayden Creek Picnic Ground) and Wet Mtn. Valley drainage (near Rosita, 9200'), probable Huerfano Park and possible San Luis Valley drainage, 6000-usually 8400', mostly in canyon bottoms. One brood, May 11-July 11 (mostly May 25-June 30). Uncommon. Larval hosts legumes.

T. mexicana nevada Scud. 35 loc: throughout the mountains (absent on the Wet Mtn. and San Luis Valley floors), 7000-12500' (usually below 10700'), in aspen parkland, and occasionally above timberline in both ranges. One brood, May 29-June 29 foothills, June 3-Aug. 1 elsewhere (usually July above 10000'). Uncommon-common. Larval hosts legumes.

Erynnis icelus (Scud. & Burgess) 21 loc: throughout the mountains, 7000-10000', near *Populus tremuloides*. One brood, mid May-June 26 at lower altitudes, May 24-July 14 elsewhere. Uncommon. Larval host *Populus tremuloides*.

E. brizo burgessi (Skin.) 30 loc: foothills and adjacent plains, Arkansas Canyon, northern Wet Mtn. Valley (11 mi. NE Silver Cliff; a record for Hermit Lake road may refer to *icelus*), and San Luis Valley drainage (Garner Creek), probable Huerfano Park, 5800-8800', near *Quercus gambellii*. One brood, April 13-June 8 (extreme June 21) foothills, four records April 25-July 12 elsewhere. Common. Larval host *Q. gambellii*.

E. telemachus Burns 59 loc: throughout the mountains including the plains-foothills ecotone, south in the Wet Mtn. Valley drainage to Bull Domingo Hills, north in San Luis Valley drainage to Ferguson Creek. 5800-8500', near *Quercus gambellii*. One brood, April 13-July 11 foothills, April 25-Aug. 4 (usually mid May-mid July) elsewhere. Common. Larval host *Q. gambellii*.

E. horatius (Scud. & Burgess) 21 loc: foothills and plains-foothills ecotone, Arkansas Canyon, and Wet Mtn. Valley drainage south to Bull Domingo Hills, probable Huerfano Park, possible San Luis drainage (present along the Rio Grande farther south), 5600-8400', near *Quercus gambellii*. Two broods, April 13-May 26, June 22-Aug. 26 foothills, second and probably the first brood slightly later elsewhere, July 24-Aug. 24. Uncommon. Larval host *Quercus gambellii*.

E. zarucco funeralis (Scud. & Burgess) Two migrants from farther south were caught at Hardscrabble Canyon (Sept. 4, Robert Price, oral commun. 1971) and Pueblo (Nash, 1893). The species apparently cannot overwinter here.

E. martialis (Scud.) 3 loc: Wet Mtn. foothills (near and north of Beulah) and Huerfano Park (La Veta), 6400-7000' near *Ceanothus fendleri*. One brood, May 7-mid June (rarely to July). Uncommon. Larval host *C. fendleri*.

E. pacuvius (Lint.) 15 loc: foothills, Arkansas Canyon (Hayden Creek Campground), all along both sides of the Wet Mtn. Valley (Music Pass Road, Rosita), San Luis Valley drainage (Music Pass, Mt. Blanca), probable Huerfano Park. 6400-9400', in chaparral and pine woodland.

One brood, May 7-July 6 foothills, May 26-July 30 (once Aug. 10) elsewhere. Uncommon. Larval host *Ceanothus fendleri.*

E. persius fredericki Freeman 57 loc: throughout the mountains, but rare in plains-foothills ecotone (near Stinking Spring), several records along streams on the Wet Mtn. and San Luis Valley floors, 6000-12349' (usually below 10500', but 9 records above 10300' in all three ranges). One brood, May 25-July 11 foothills, May 25-Aug. 1 (once Aug. 16) elsewhere. Common. Larval hosts legumes in western U.S. including *Astragalus* sp. probably *bisulcatus* (oviposition at Rosita).

E. afranius (Lint.) 11 loc: plains within 5 miles of the mountains, the foothills, Arkansas Canyon, probable lower Huerfano Park. Present in Rio Grande drainage farther south in New Mexico, but apparently not in San Luis Valley here. 5500-7000', in prairie gulches and pinon-juniper woodland. Two broods, April 23-May 19, July 2-Aug. 1 (late records Aug. 16 and Sept. 5). Uncommon. Larval hosts legumes including *Lupinus argenteus* and *Astragalus*; *Lupinus* does not occur at several plains localities so another legume must be used there.

Pholisora alpheus (Edw.) 14 loc: plains west to the foothills and east to La Junta, Arkansas Canyon, Huerfano Park, and San Luis Valley floor (Saguache and Manassa), 4300-7700', in gulches and alkaline flats near *Atriplex canescens*. Apparently two broods, May 15-June 23 (worn), July 3-Aug. 5 (worn) plains (a third brood may occur on the plains), so far only June 8-24 in Arkansas Canyon and San Luis Valley. Uncommon, rarely abundant. Larval host *A. canescens*. Adults feed on *Medicago* and other flowers. Some individuals here resemble the western slope subspecies.

P. catullus (Fabr.) 27 loc: plains, foothills, Arkansas Canyon, Wet Mtn. Valley floor south to Lake Creek, Huerfano Park, San Luis Valley floor (SE Monte Vista), 4300-8900' (usually below 7600'), along roadsides and railroad tracks, and in gulch bottoms. Dates almost continuous from May 10-Sept. 8 on the plains-foothills may represent three broods. Two broods Arkansas Canyon, June 12-27, July 30-Sept. 10. Perhaps one brood, June 21-July 28 elsewhere. Uncommon, sometimes common. Larval hosts Chenopodiaceae and Amaranthaceae in Colorado including *Chenopodium album*, *Amaranthus retroflexus* (larvae raised from El Paso Co.), *A. graecizans*, *A. albus*. 35 Colorado larvae placed on *Marrubium vulgare*, *Verbena bracteata*, *Monarda* sp., and *Ambrosia* sp., all published or suspected hosts in other plant families, did not eat any of these four plants.

P. mejicana (Reak.) 6 loc: north half of the Wet Mtn. foothills, and the Arkansas Canyon. Probable lower Huerfano Park and possible on the plains (present on the plains next to the mountains near Colorado

Springs), 6600-7400', in gulch bottoms, along railroad tracks, always sympatric with *catullus* and with identical behavior. Two broods, June 3-July 7, July 15-Aug. 26. Uncommon, rarely abundant. Larvae feed on *Amaranthus retroflexus* (larvae raised to adults from N. of Colorado Springs, El Paso Co.) and *A. graecizans* (oviposition Kerr Gulch, Fremont Co.). First instar larvae will eat test leaves of *Chenopodium album*, and K. Roever reports *Chenopodium* as the foodplant in New Mexico, but this plant is not attacked in El Paso Co. where *A. retroflexus* plants may have up to 8 larvae. Adults feed mainly on low flowers (blue *Verbena bracteata, Lappula redowskii, Cirsium arvense*, etc.) and mud. *P. catullus* and *mejicana* have identical behavior and adult and larval foodplants (I reared both from the same plant) yet they continue to coexist.

Pyrgus centaureae loki Evans 6 loc: Wet Mts. (Greenhorn Peak to 10 mi. NW) and Sangre de Cristo Mts. (Hermit Pass, Baldy Peak, West Creek Lake), 10500-13000', in subalpine and alpine meadows. One brood, June 21-Aug. 11. Uncommon. Larvae feed on *Potentilla diversifolia* in Colorado, and on *Fragaria* elsewhere. *Epargyreus, Thorybes, Erynnis*, and *Pholisora* adults feed on flowers of all colors; *Pyrgus* seems to visit yellow flowers slightly more than other colors.

P. scriptura Bois. 21 loc: plains, foothills edge, Arkansas Canyon, Wet Mtn. Valley floor south to south of Silver Cliff, probable Huerfano Park, the San Luis Valley floor and hills north to west of Villa Grove. 4700-8400', on prairie or open pinon-juniper woodland. Three broods on plains, and perhaps in Arkansas Canyon, April 28-late May, June 16-July 22, late Aug.-mid Sept. Two broods in Wet Mtn. Valley, mid May-mid June, July 15-Aug. 22. Uncommon. Larval hosts Malvaceae including *Sphaeralcea coccinea* in Colorado.

P. xanthus Edw. 7 loc: Wet Mts. (Custer and Huerfano Counties), Sangre de Cristo Mts. (Poncha Pass) and Cochetopa Hills, 8900-10500', in grassland or openings in forest. One brood, May 26-June 20 (extremes May 3-July 3). Uncommon. Larval hosts *Potentilla* (Scott 1975a), associated with *P. hippiana* (misidentified by botanists as *P. anserina* when reported by Scott 1975a) in southern Colorado and the Pueblo area. Adults feed on *Taraxacum*, mud, manure, etc. Nash's (1893) record of *P. ruralis* from Rosita undoubtedly refers to *xanthus* which flies there.

P. communis (Grote) 42 loc: throughout the area, 4300-10800' (usually below 9000'). About four broods plains, May 11-June 3, June 13-July 5, July 22-Aug. 17, Sept. 2-Oct. Records are very similar elsewhere except there are fewer May (27-28) and Sept. (10-19) records. Common. Larval hosts Malvaceae including *Sphaeralcea coccinea* in dry plains (ovipositions Westcliffe and Bull Domingo Hills in Custer Co.), *Malva neglecta* in disturbed areas (oviposition Coaldale in Fremont Co.), and *Sidalcea neomexicana* in wet meadows.

Piruna pirus (Edw.) 34 loc: throughout the mountains, south in Wet Mtn. Valley drainage to Bull Domingo Hills (and supposedly Music Pass, Nash 1893), north around San Luis Valley to mountains east and west of Villa Grove, in Huerfano Park along streams. 6400-9000', in moist valley bottoms. One brood, June 4-July 11 (once Aug. 2) foothills, June 5-July 29 Arkansas Canyon, June 22-Aug. 9 San Luis Valley. Usually uncommon, common in San Luis Valley. Larval hosts probably valley bottom grasses such as *Poa*. Adults feed on flowers of all colors, mainly blue.

Oarisma garita (Reak.) 40 loc: throughout the mountains, absent in the Arkansas Canyon bottom, 6400-10500'. One brood, June 20-July 13 foothills, June 24-Aug. 1 (extreme Aug. 12) elsewhere. Common. Larval hosts grasses including *Sitanion hystrix* (oviposition Round Mountain, Custer Co.), *Blepharoneuron tricholepis* (oviposition NE Rosita), *Stipa columbiana* (oviposition Bull Domingo Hills). Adults feed on various flowers of all colors, often yellow *Compositae*.

O. edwardsii (Barnes) 12 loc: Wet Mtn. foothills and Arkansas Canyon, probable Huerfano Park, 6400-7500', in openings in chaparral and woodland, often in drier areas than *garita*. One brood, June 20-July 17 foothills, July 1-25 Arkansas Canyon. Uncommon, sometimes common. Larvae probably feed on grasses. Adults feed on many flowers of all colors: *Astragalus, Geranium, Lesquerella, Linum, Ceanothus, Penstemon, Apocynum*, etc.

Yvretta rhesus (Edw.) 20 loc: plains, lower foothills, Arkansas Canyon, Wet Mtn. Valley bottom south to Westcliffe and Rosita, San Luis Valley bottom north to 9 mi. NW Villa Grove, probable Huerfano Park, 4300-8400' (one record 9000'), on prairie or open pinon-juniper woodland. One brood, April 30-June 4 plains-foothills, May 20-June 25 (worn) elsewhere. Uncommon. Larvae lay eggs on *Bouteloua gracilis*. Adults feed mainly on whitish *Astragalus drummondi* flowers.

Stinga morrisoni (Edw.) 15 loc: Wet Mts. (only two records in the foothills, south of Canon City and Phantom Canyon), Arkansas Canyon, hills in Wet Mtn. Valley south to Bull Domingo Hills, Huerfano Park, around San Luis Valley north to Hayden Pass Creek, 6000-9600' (usually 7000-8700'), pinon-juniper or ponderosa forest. One brood, May 3-June 24 foothills, May 24-July 3 (rarely 15) elsewhere, Usually uncommon, common in San Luis Valley. Larvae probably feed on various grasses. Adults of *Stinga* and the following Hesperiinae unless otherwise noted often feed on flowers, such as reddish blue *Cirsium*, *Medicago*, *Monarda*, *Lonicera*, sometimes on yellow *Opuntia*, *Solidago*, etc., and on mud.

Hesperia uncas Edw. 39 loc: plains, foothills edge, Arkansas Canyon, Wet Mtn. Valley floor and bordering hills, Huerfano Park, and San Luis Valley floor and occasionally the bordering hills, 4300-9000' (9800' at Lapin Creek in Wet Mts.; 12500' Galena Peak and 13000' Hermit Pass in Sangre de Cristo Mts., possibly breeding there), on prairie and pinon-Juniper woodland. Two broods on the plains-foothills, May 25-June 22, July 31-Aug. 30, several records between these dates. Apparently one brood elsewhere, June 11-Aug. 4 (extreme Aug. 24). Common. Larval hosts *Bouteloua gracilis* (three ovipositions near Westcliffe, Custer Co., one near Salida, Chaffee Co.).

H. comma (Linn.) *ssp.* 46 loc: throughout the mountains including the hills in the Wet Mtn. Valley (Bull Domingo Hills, Promontory Divide), 6500-9000' (rarely 9600'), in woodland or prairie. One brood, July 28-Sept. 10 (extremes July 21-Sept. 26). Common. Larval hosts probably various grasses, but females oviposit haphazardly on grasses, sedges, and *Arenaria* (a dicotyledon resembling grass) (Scott 1975b). *H. comma* occurs on the plains near the Black Forest in the Arkansas-South Platte River divide, but not on the plains here. Specimens from our area are an undescribed subspecies with bright yellow ventral hindwing with a silver chevron, which intergrades with subspecies *colorado* (which does not occur here) between Buena Vista and Tennessee Pass, and in the mountains west of the San Luis Valley (Scott 1975b).

H. leonardus pawnee Dodge. 3 loc: plains near the mountains, 6000-6600', on prairie habitats. One brood, mid Aug.-mid Sept. Common. Larval hosts grasses. Specimens have slightly larger traces of ventral hindwing spots here than elsewhere on the Colorado plains. Adults feed mainly on *Liatris punctata*, which blooms at the same times and location as the butterfly.

H. pahaska Leussler 43 loc: throughout the mountains including the plains-foothills ecotone, S in Wet Mtn. Valley hills to Rosita, N in San Luis Valley hills to Hayden Pass Creek, 5600-9600' (usually below 9000'), in chaparral or woodland. One brood, June 3-July 13 foothills, June 9-July 29 (ocasionally to Aug. 17) Arkansas Canyon, June 12-Aug. 4 (once Aug. 16) elsewhere. Common. Larval host mainly *Bouteloua gracilis* (ovipositions Bear Creek, Chaffee Co., Scott 1974a).

H. viridis (Edw.) 54 loc: throughout the area, south in hilly areas of Wet Mtn. Valley to Bull Domingo Hills, N in San Luis Valley floor so far only to the Sand Dunes, 4300-8200', on prairie, chaparral, woodland. Two or three broods on the plains, May 25-June 18, July 7-Aug. 5, records Aug. 13 and Sept. 2 may represent a partial third brood. Two broods in Arkansas Canyon and the Wet Mtn. foothills, May 30-July 3, July 10-Aug. 7, and scattered records until Sept. 10. One brood Wet Mtn. and San Luis Valleys, June 30-July 28 (once Aug. 18). Common. Larval hosts *Bouteloua gracilis* (ovipositions Bear Creek, Chaffee Co., Scott 1974a).

H. nevada (Scud.) 33 loc: throughout the Wet, Sangre de Cristo, and Cochetopa Mts., extending into Wet Mtn. Valley drainage to Ben West Hill and Promontory Divide, and to the edge of the San Luis Valley NE of Fort Garland, 6800-10500' (rarely up to 11500'), most often in aspen parkland. One brood, mostly June 14-July 10 (extremes May 26-Aug. 16), June 15-July 27 above 10500'. Common. Larval hosts grasses including *Koeleria* (oviposition at Rosita, Custer Co.).

Polites sonora utahensis (Skin.) 3 loc: around the San Luis Valley (Ferguson Creek, W of Saguache, W of Villa Grove); also present 3 miles south of Buena Vista just north of the area and north of the Arkansas Canyon, 8200-9800', in moist meadows almost always with *Cirsium drummondi* var. *acaulescens*. Such meadows occur in the Wet Mts. and Wet Mtn. Valley, but numerous trips have failed to produce it there. One brood, July 19-Aug. 22. Uncommon-common. Larvae probably feed on wet meadow grasses; adults feed mainly on *acaulescens*, occasionally on other flowers such as *Taraxacum*, and on manure and mud.

P. sabuleti (Bois) *ssp.* 8 loc: San Luis Valley floor north to San Isabel Creek, and the upper Arkansas Canyon, 6600-7800', in moist meadows where *Eragrostis trichodes* is common. One brood, June 17-late July, occasionally to Aug. 6. Common. Larval hosts *E. trichodes* (oviposition on *E. trichodes*, 11 eggs found on. *trichodes*, 5 on *Equisetum*, 1 on a dicotyledon, all growing near *trichodes* in the Arkansas River Canyon). Adults feed on *Medicago, Polygonum, Aster*, etc. Adults lack the dark post-stigmal patch present in Great Basin specimens. Ground color of the wings is lighter in Pueblo area specimens than in Great Basin specimens; ground color is slightly lighter in the San Luis Valley specimens than in Arkansas Canyon specimens.

P. draco (Edw.) 48 loc: all three mountain ranges, 8400-12500' (7800' at Hayden Creek Campground, infrequent above 11500'), in moist swales and valley bottoms. One brood, June 19-Aug. 1 (extremes May 28-Aug. 23). Uncommon. Larvae feed on unknown monocotyledons. Adults feed on various yellow and blue composites, etc.

P. themistocles (Latr.) 27 loc: Wet Mts. (mainly the foothills), Wet Mtn. Valley floor (one record 8 mi. E. Westcliffe), Huerfano Park, Arkansas Canyon, San Luis Valley drainage (5 mi. S. Poncha Pass: Medano Creek), 6600-9000', in moist meadows or moist valley bottoms. Absent on plains, even though it feeds on lawns on the plains northward at Denver, where it has two broods. One brood in the Pueblo area, June 12-July 11 foothills and Arkansas Canyon (late records July 17, Aug. 8 and 24 in Arkansas Canyon), June 27-Aug. 1 (late records Aug. 10 & 28) elsewhere. Uncommon-common. Larval hosts grasses.

P. origenes rhena (Edw.) 7 loc: Wet Mtn. foothills, 6600-7600', in valley bottoms with tall grasses including *Poa* sp. One brood, June 20-July 13. Uncommon, abundant once. Larval hosts grasses.

Atrytone delaware (Edw.) 1 loc: Wet Mtn. foothills (Oak Creek Canyon, syntype of *lagus*), possible on moister areas of the plains in wet tall-grass valley bottoms. One brood, June 25-July 25. Locally common. Larval hosts grasses.

Ochlodes snowi (Edw.) 18 loc: Wet Mts. above the foothills (a record from "Beulah", is undoubtedly from higher mountains), Arkansas Canyon above the bottom, Sangre de Cristo Mts. west of Huerfano Park, and hills surrounding San Luis Valley, apparently absent on hills west of Wet Mtn. Valley due to heavy forest, 7500-9600', mainly in upper edge of the *Pinus ponderosa* belt. One brood, July 12-Aug. 4 (peak late July, once Aug. 9). Uncommon, occasionally abundant. Oviposition is on *Blepharoneuron tricholepis* (Rosita, Custer Co., Scott 1974a). Adults feed mainly on blue-purple flowers, especially legumes (*Oxytropis*, *Astragalus*, etc.) and *Penstemon.*

Poanes hobomok (Harris) *ssp.* 10 loc: throughout the Wet Mtn. foothills and foothills-plains ecotone from near Rye to Oak Creek, including the divide between South Hardscrabble Creek and North Creek, 6000-7800', in dense oak-ponderosa-*Poa* habitat, rarely in open areas. It also occurs south of the area on Raton Mesa; elsewhere it only occurs in eastern U.S. west to Nebraska. One brood, May 25-July 7 (peak about June 20; a May 5 record at plains-foothills ecotone in 1972, a very early season). Common. Larval hosts grasses. This population is slightly lighter with slightly narrower dark wing borders and less sexual dimorphism than eastern U.S. specimens.

P. taxiles (Edw.) 45 loc: throughout the mountains, hills in the Wet

Mtn. Valley south to Bull Domingo Hills, mountains surrounding San Luis Valley north to Hayden Pass Creek, and on the plains along streams east to Pueblo, 4800-8800', in valley bottoms and in cottonwood groves, usually in semi-shaded areas, and flying in cloudier weather than *P.hobomok*. One brood, June 17-Aug. 2 (extremes June 12-Aug. 9) Common. Oviposition is known on four species of grasses in Colorado including *Puccinellia airoides* and *Agropyron smithii.*

Euphyes vestris metacomet (Harris). 52 loc: foothills down to the plains, the Arkansas Canyon, Wet Mtn. Valley hills south to Bull Domingo Hills and Rosita, Huerfano Park. Probable San Luis Valley (known near Mosca Pass, a possible sight record Hayden Pass Creek) as it is present farther south. 5800-9000', (usually below 8500') in moist canyon bottoms. One brood, June 12-Aug. 3 (June 4-Aug. 25 Arkansas Canyon). Common. Larval hosts sedges including *Carex heliophila* in Colorado. Adults feed on various flowers and also on bird droppings.

Atalopedes campestris (Bois.) 10 loc: plains, foothills, and all along the Arkansas Canyon, probable Huerfano Park. 4300-7600', mainly on flats in valley bottoms where *Eragrostis* is common, and in suburbs of towns. A record from Ophir Creek, 9800' (Aug. 25) in Wet Mts. suggests considerable dispersal, but the species may be native on the plains. Three or four broods on the plains, June 12-24 (once May 8), July 7-Sept. 12 (perhaps 2 broods), Oct. 1-Nov. 2. One brood June 10-Aug. 6 Arkansas Canyon. Uncommon. Larval hosts grasses.

Amblyscirtes simius (Edw.) 24 loc: plains, northern Wet Mtn. foothills south to Oak Creek, Arkansas Canyon, Wet Mtn. Valley (Bull Domingo Hills), San Luis Valley hills north to W of Villa Grove, probable Huerfano Park, 4800-8400' (one record 9000' NE of Salida), in prairie and pinon-juniper woodland. One brood, June 3-25 (sometimes July 5) plains, June 9-30 (once July 11) Arkansas Canyon, 5 dates July 8 to rarely Aug. 2 above 8000'. Uncommon, sometimes abundant. Larval host *Bouteloua gracilis* (Bear Creek, Chaffee Co., Scott 1973a).

A. phylace (Edw.) One male in the foothills N of Arkansas River (Phantom Canyon, 6500', M. Howard), a female on divide at head of Pass Creek, Huerfano Co. (9200'); the species may occur throughout the mountains. In the Front Range it occurs only in foothills and in the Black Forest, but southward it occurs at higher elevations. One brood, May 21-July 7. All *Amblyscirtes* larvae undoubtedly feed on grasses, including *Poa* in the laboratory for *A. aenus*.

A. eos (Edw.) 8 loc: plains and foothills edge, 4500-6000'. Perhaps three broods, May 5-31, July 3-Aug. 1, Sept. 8. Uncommon-rare, on prairie and chaparral. This species may have invaded southeastern Colorado recently.

A. aenus Edw. 17 loc: Wet Mtn. foothills, Arkansas Canyon, probable Huerfano Park (on the moister plains south of our area), 6000-7300', in canyons and gulches. One brood, May 11-June 24 (extremes April 23-July 4) foothills, late May-June 24 Arkansas Canyon. Uncommon.

A. vialis (Edw.) 12 loc: Wet Mtn. foothills, foothills-plains ecotone, Arkansas Canyon, probable Huerfano Park, 6000-7800', in moister valley bottoms usually with *Quercus* and *Poa* sp. One brood, May 5-July 17 (peak mid June) foothills, June 12-July 17 Arkansas Canyon. Uncommon.

A. oslari (Skin.) 25 loc: plains SW of Pueblo, in the Wet Mtn. foothills, foothills-plains ecotone, Arkansas Canyon, Wet Mtn. Valley drainage (Bull Domingo Hills eastward to Junkins Park and the Road to Locke Park), probable Huerfano Park, 5200-9800', usually in gulches. One brood, April 28-July 13 foothills-plains, records June 4-25 elsewhere. Uncommon-common.

Atrytonopsis hianna turneri Freeman. 9 loc: throughout the Wet Mtn. foothills, 6000-7200', in *Quercus* habitat in canyons. One brood, May 4-June 30. Uncommon-common. Larval host *Andropogon gerardi, A. scoparius*.

Atrytonopsis vierecki (Skin.) 12 loc: plains, Arkansas Canyon west at least to Cotopaxi, the Wet Mtn. foothills only near Canon City (N. of Chandler to Phantom Canyon), probable Huerfano Park, never flies with *A. hianna*, 5100-7500', in prairie and pinon-juniper gulches. One brood, May 20-July 4. Uncommon-common. Larvae probably feed on grasses.

Megathymus yuccae coloradensis (Skin.) 6 loc: San Luis Valley hills and floor, Arkansas Canyon (Buena Vista), Wet Mtn. Valley (Rosita, Nash, 1893), foothills (Phantom Canyon), probable on plains and Huerfano Park, 6400-9000', on prairie and pinon-juniper habitat. One brood, May 3-June 2. Uncommon-rare. Larvae feed on various *Yucca* species (tents found east of Villa Grove). Adult *Megathymus* never feed.

M. streckeri. 13 loc: plains, Arkansas Canyon, Huerfano Park (subspecies near *texanus* B. & McD.) and San Luis Valley hills and floor north to W of Villa Grove (subspecies *streckeri* (Skin.), 4300-8400', in prairie and pinon-juniper habitat. One brood, May 26-July 14 plains, June 14-July 24 elsewhere. Uncommon, sometimes common. Larvae feed on various *Yucca* species.

Discussion

Possible Additional or Erroneously Recorded Species

Several species possibly occur in the Pueblo area. *Callophrys sheridanii* occurs on Mt. Elbert, 12000', in the Saguache Range NW of the area (Samuel Johnson collector) and in southern New Mexico. *Oeneis polixenes* occurs in the Front Range and in the Sangre de Cristo Mts. in New Mexico. Isolated relict populations of these two species possibly occur in the Pueblo area. *Speyeria cybele* and *S. hydaspe* occur in the Sangre de Cristo Mts. in New Mexico but not in Colorado. *S. nokomis* occurs on both sides of the Sangre de Cristo Mts. in New Mexico but has not been found at apparently suitable springs in the Pueblo area. *Euchloe hyantis* approaches the area along the Rio Grande farther south in New Mexico. An introduced colony of *Lycaena phlaeas* occurred once (2 specimens) near Colorado Springs NE of this area. *Polites coras* has invaded the Denver area recently and several were caught in Gunnison and Saguache Counties west of the area. Other Front Range species' distributions stop within 50-100 miles of the area (most of these stop more than 30 miles north of the area) but have not been found in the Pueblo area despite intensive search: *Speyeria callippe, Chlosyne palla, Phyciodes pallida, Satyrium californica* and *saepium, Hesperia juba* and *ottoe, Polites mystic, Atrytone arogos*, and *Ochlodes sylvanoides*. *Papilio indra indra* also was not found (a fresh male in F. M. Brown collection labelled Sand Dunes N. Mon., 8100', 23-vii-34, collection of Bob Potts, may be mislabelled because there are no other records south of Denver, and this subspecies flies only in May and June). *Euphilotes enoptes* does occur in Chaffee County (Silver Plume Creek, 9600') just north of the Pueblo area. However, a record from La Veta Pass (Brown el al. 1957) is very dubious: the specimens have burned, identification by wing pattern is difficult, and we have not found it there. Its usual host *Eriogonum umbellatum* does occur at La Veta Pass, at Promontory Divide, and near Westcliffe but is rare. Several high altitude species occur along the continental divide in Colorado, but not in the Sangre de Cristo Mts: *Erebia callias* and *theano, Boloria frigga* and *eunomia*. One male *Oeneis taygete* from Hermit Pass in the Sangre de Cristo Mts., July 29, was found by Maurice Howard. Because of a possibility of label confusion and because this locality has been sampled a dozen times without seeing others, verification is needed. A female recorded as *Plebejus argyrognomon* from Pass Creek (Brown et al. 1957) was since burned, but very probably was *P. melissa*. Nabokov (1949) discusses a female from San Isabel Forest above Beulah, 7500', leg. Stallings, which he questionably determines as *argyrognomon*. This record is also dubious; the male genitalia is the only reliable character for identifying Colorado *argyrognomon*. *P. argyrognomon* may occur in Cochetopa Hills west of the San Luis Valley. *Oeneis jutta* has been found 3 and 8 mi. N. of Sargents in Gunnison Co. Colorado, and may occur in the Cochetopa Hills in this area. *Copaeodes aurantiaca*, *Ancyloxypha numitor*, and *Euristrymon ontario* occur just southeast of the Pueblo area. At least ten species from Texas occur as strays elsewhere in Colorado and will eventually be found in the Pueblo area.

Geographic Distribution Within the Area

178 species, 160 native and 18 temporary strays, occur in the area. At least 17 other species stray into Colorado and may eventually be found.

The temporary species are all native in Texas, and some are native to New Mexico and Arizona. They are found most often on the plains and lower foothills in the eastern part of the area, less often in the Arkansas Canyon bottom, and rarely in the rest of the area. They evidently arrive mainly from the southeast, especially Texas.

The Wet Mountain foothills have the richest fauna: ignoring strays and the 12 subalpine or alpine species, the foothills from 6000-8000 ft. have 121 species, the Arkansas Canyon (up to 9000 ft.) has 117, the Wet Mountain Valley and its hills (to 9000 ft.) has 114, San Luis Valley and hills (to 9000 ft.) have 113, the plains only have 62 (but many others occur in the plains-foothills ecotone). Fig. 2 illustrates the richness of foothills altitudes.

Distribution within the area seems to depend mainly on climate and suitable habitats rather than on barriers to movement. Alpine species are now apparently unable to disperse from the Sangre de Cristo Mountains to the Wet Mountains. The major barrier to movement of lowland butterflies in the area is the high Sangre de Cristo Range, but this barrier has very seldom impeded the movement of the butterflies (Table 1). Most of the species are quite widespread (Table 1, group 1). These, and most of the others (Table 1, group 2), are distributed in a manner obviously consistent with altitude/temperature gradients (see the climate section below).

Several species superficially seem restricted in distribution due to the Sangre de Cristo Mountains acting as a barrier (Table 1, group 3). This is because the San Luis Valley and Wet Mountains Valley are nearly equivalent in altitude, mean annual temperature, habitats, and in most butterfly species. However, all of the species in group 3 except *L. hyllus*, *S. liparops*, *P. sonora*, and *O. alberta* are present south of the San Luis Valley in the Rio Grande Valley, so that absence in the San

Luis Valley is generally due to the climatic unsuitablity of its high elevation. *S. liparops* is present in Gunnison County on the western slope, and may possibly occur in the San Luis Valley. *P. sonora* may have occurred in the Wet Mountain Valley drainage, and then became extinct there. *C. meadii* and *O. alberta* are species which, judging from their widespread but spotty distributions, were formerly widespread but became extinct in all but a few parts of their former range. The larval foodplant of *E. spaldingi* occurs only in the southern San Luis Valley along with the butterfly, but does not reach this area. Therefore, only *L. hyllus* and perhaps *S. liparops* and *P. sonora* seem to be restricted in distribution by being unable to cross the Sangre de Cristo Mountains. Chance dispersal of most butterflies apparently permits them to cross this barrier at low points such as Mosca, Medano, La Veta, Hayden, and Poncha Passes.

Effect of present climate on distribution

Climate varies greatly within the area, and many of the distributions of the species are highly correlated with climatic gradients, especially gradients in temperature. Frost-free period varies from 5.5 months on the plains to less than 2 months in the alpine zone. Mean annual precipitation is lowest in the San Luis Valley (about 9 inches), is about 12 inches on the plains and in Arkansas Canyon at Salida, and 15 inches at Westcliffe (7800 ft.) in the Wet Mountain Valley. It is higher in the mountains: 23 inches at Wetmore (6050 ft.), 30 inches at Rye (6800 ft.) and Fairview (9500 ft.) all in the Wet Mountains, and 24 inches on La Veta Pass (9242 ft.), 41 inches at Hermit Lake (10,000 ft.), both in the Sangre de Cristo Mountains, and probably 30-50 inches at high altitudes in both ranges. Mean annual temperature is better correlated with altitude than is precipitation. It is 51°F at Pueblo, 53°F in Canon City (climate is milder at Canon City than elsewhere because of up and down canyon wind movements in the Royal Gorge), 49° at Wetmore, 47° at Rye, 45° at Salida, 43-44° at Westcliffe and in the San Luis Valley, and about 26° above timberline.

Distributions within the area are very consistent with altitudinal temperature gradients. These factors are apparently the major determinants of distribution, while precipitation seems less important. The San Luis Valley fauna is very similar to the Wet Mountain Valley fauna, and many species extend into these valleys to about the same altitude, 8400 ft. (north to west of Villa Gròve, and south to Bull Domingo Hills, respectively). The plains along the Arkansas River are lower altitude, hotter and drier than the plains to the north and south. At least 20 species extend farther east of the mountains north of this area (in the Black Forest), and farther eastward along the high mesas of the southern border of the state than they do in the the Pueblo area.

Effect of past climate on distribution

There are now large areas separating the localities where some butterflies occur. The alpine and subalpine species, especially, occur in isolated areas. In Colorado, isolated peaks that are now above timberline and have alpine vegetation do not have alpine species unless they are fairly high (more than 1500 ft. above timberline such as Pikes Peak and Spanish Peaks). Isolated peaks only 500 ft. above timberline (such as Greenhorn Peak in the Wet Mountains in the Pueblo area) do not have alpine species. We believe the explanation for this involves both the coldest glacial periods of the Pleistocene and the warmest interglacial periods. Eight subalpine or alpine species (*Boloria frigga, improba, eunomia, Plebejus argyrognomon, Oeneis polixenes* and *taygete, Erebia callias* and *theano*) are found in disjunct parts of the high mountains of the state, apparently because they became extinct in the other alpine areas for reasons other than climatic changes.

Quaternary climate has been both colder and warmer than it is now. During one late period of maximum glaciation, molluscs lived on the plains near Denver, which now live near timberline (11,500') on Pikes Peak (Scott 1963). Based on the pollen record of the southwest, Martin & Mehringer (1965, Figs. 3 & 4) show major changes in vegetation of New Mexico between "full glacial" times and now. High plains areas eastward from the mountains (even in Texas) that now are covered by grassland were during "full glacial" time covered by spruce and ponderosa pine parkland, foothill areas that now are covered by pinon-juniper woodland and ponderosa-pine parkland were covered by spruce-fir-pine forest, and high mountains areas now covered by spruce-fir-pine forest were above treeline. Glaciers in the Wet Mountains and Sangre de Cristo Range advanced as low as 8500 ft. (the altitude of modern montane glaciers in Colorado is about 12,000 ft.), several thousand feet lower than their sources. Thus, glaciation was nearly as low as the floor of the Wet Mountain Valley and San Luis Valley and alpine butterflies spread over all the mountainous parts of the area during the coldest pleistocene times. Alpine zone had to extend as low as about 7000' in southern Wyoming for alpine butterflies to enter Colorado from the north; alpine zone was therefore lowered 4000' or more from the present altitude.

On the other hand, interglacial times were sometimes warmer than now. During interglacial times, which were relatively short, the glaciers melted back to, or nearly to, their sources. The warmth of interglacial and postglacial time is shown by molluscs in one late middle Pleistocene interglacial deposit near Denver that are the same as those in Altithermal (postglacial — about 5,500 to 4,500 years before the present) deposits near Denver and the same as those now living in southern Texas, New Mexico, and Arizona (Scott 1963). During the interglacial parts of the Pleistocene and during Holocene (post-Pleistocene) time the alpine and arctic species almost certainly would have moved up into the mountains to altitudes as high or higher than they now live. For instance, greater warmth in Altithermal time than now probably caused the current absence of alpine, but not subalpine, species on Greenhorn Mountain; even though there are extensive alpine areas there now. Its altitude of only 12,349 ft. probably resulted in a climate too warm to be tolerated by alpine butterflies. Assuming that the butterflies were eliminated from the peak, they were then unable to return because the climate never again was cold enough to permit them to cross the Wet Mountain Valley from the higher Sangre de Cristo Range. During the warmest interglacial times pinon-juniper woodland probably extended nearly to the summit of low passes in the Sangre de Cristo Range such as Mosca Pass, allowing greater dispersal of lowland butterflies than is possible today.

Zoogeography of the Species in Comparison with the Remainder of Colorado

This area is warmer and drier than the Front Range area near Denver, and this is reflected in the butterfly fauna as well. Thirteen species occur at lower altitudes in the Front Range near Denver than they do in the Pueblo area, and two species which occur at mid to low altitude in the Front Range are nearly restricted to the alpine zone in the Sangre de Cristo Range. Several species which occur as two altitudinal phenotypes in the Front Range (*Lycaena rubidus, L. heteronea, Hesperia comma*) are represented here only by the low-altitude phenotype.

Another phenomenon of distribution in Colorado seems to involve the same meteorological phenomenon. Nine species are missing in the foothills and plains area near Denver, but fly in areas both north and south of Denver (*Satyrium sylvinus, Chlosyne acastus, Cercyonis meadii, Euphilotes rita, Apodemia mormo, Amblyscirtes simius, Yvretta rhesus, Atrytonopsis hianna, Megathymus streckeri*). These species occur in the Arkansas Valley area and usually near Colorado Springs, are absent in the Denver area and usually in the Black Forest north of Colorado Springs, then reappear northward in Larimer County, Colorado (which is drier), southeastern Wyoming, or in the case of *M.*

streckeri, in Montana. Several of these species occur continuously around the circumvented Denver area.

The Black Forest is a higher eastern extension of the ponderosa pine forest between the Pueblo area and Denver to the north. Some species circumvent but are missing in the Black Forest apparently because it is too cold, and at least 16 species extend farther east of the mountains in the Black Forest than they do along the Arkansas River.

The Pueblo area contains 178 of the 247 species known for Colorado, or 72%. The distributions of the 247 Colorado species are listed in Table 2. The area east of the Continental Divide is somewhat richer than the area west of it, but there is very little difference in species richness in the north or south. There is no abrupt north-south break in species distributions, instead there is a gradual change in species composition north to south.

The distribution east of the divide of those species also occurring west of it was analyzed. The number of these west-slope species varies by only 2 or less in any area along the eastern slope mountains and adjacent plains. Therefore the faunas of the Pueblo area and of the Front Range are about equally related to the western slope, in spite of gradual change in composition of western-slope species along the eastern slope corridor. For instance, 18 west-slope species occur in the Pueblo area, but not in Larimer County on the northern edge of the state, and 16 west-slope species occur in Larimer County, but not in the Pueblo area.

To determine the relationship between the fauna of the Pueblo area and the rest of North America, distributions of the 160 native species were analyzed: 25 species are widespread in the U.S.; 61 occur only in western North America and sometimes (17) extend eastward across southern Canada, 17 occur mainly in the Rocky Mountains, 34 occur in southwestern U.S., 5 occur in eastern and southern U.S., and 18 occur mainly in eastern U.S. (6 only northeastward). These data clearly show that the fauna is western, with a smaller amount of other elements.

Geographic Variation

Eleven species have a different phenotype in the Pueblo area than elsewhere: *Hesperia comma, Polites sabuleti, Poanes hobomok, Oeneis alberta, Cercyonis meadii, Chlosyne damoetas, C. acastus, Apodemia mormo, Callophrys mossii, Celastrina argiolus, and Euphilotes spaldingi.* Five species differ geographically within the area: *Megathymus yuccae, M. streckeri, Speyeria atlantis, Cercyonis pegala,* and *Plebejus shasta.* Four species have different altitudinal forms: *Parnassius phoebus, Euphydryas chalcedona anicia, Lycaena helloides,* and *Plebejus acmon.* Details are given under the species accounts.

Species restricted to few habitats

Butterfly "communities" do not exist except as statistical associations of species with similar climate requirements or resources (foodplants). Below we mention those species most restricted to a conspicuous type of vegetation association. There are of course other associations between butterflies and plants due to their restricted feeding habits.

1. Alpine zone. Four strictly alpine species occur in the Pueblo area: *O. melissa, E. magdalena, C. damoetas, L. cupreus.* Three others (*P. shasta, C. meadii,* and *P. centaureae*) are alpine and subalpine. Only the latter three species are in the Wet Mountains. Perhaps the four alpine species did extend to the Wet Mountains (Greenhorn Peak is 12,349 ft. and above timberline) in the Pleistocene, but became extinct during the warmer period following the last glacial advance. The Sangre de Cristo Mountains north of Hayden Pass are narrower and are poorer collecting than south of the pass, but all of these seven species except *O. melissa* are known north (in addition to south) of this pass.
2. Riparian habitats. Many species occur mostly along riparian vegetation (growing along streams) or wet meadows, including *P. rutulus, P. multicaudata, C. scudderii, P. napi, D. plexippus, L. archippus, L. wiedemeyerii, P. faunus, N. antiopa, S. atlantis, P. tharos, C. nycteis, B. freija, B. selene, S. sylvinus, S. acadica, L. rubidus, L. helloides, L. hyllus, L. xanthoides, P. saepiolus, E. comyntas, P. pirus,* and *A. delaware.* These species feed as larvae on plants growing along streams or in wet meadows.
3. Pinon-juniper woodland. Many species occur in this woodland, but the only species that are mostly restricted to it are *P. bairdii, C. acastus, E. dorothea, C. nelsoni, E. spaldingi, S. morrisoni, H. pahaska.*
4. Chaparral. *S. behrii* and *O. edwardsii* occur mostly in *Cercocarpus* chaparral.
5. Grassland. Only a few species seem mostly restricted to grasslands, or at least to grassland areas with few to no trees: *P. scriptura, Y. urhesus, H. uncas, H. leonardus*. The first three occur on grasslands from the plains to the intermountain parks. Many more species occur mostly in medium altitude grasslands where aspen groves are frequent in moist swales: *T. mexicana, H. nevada, E. icelus, E. persius, P. xanthus, P. sonora, P. draco, C. alexandra, O. uhleri, O. alberta.*

Effect of geology on distribution of butterflies

Geology seems to effect distribution of a few species. The directness of the link between a butterfly species and geology varies greatly from a butterfly species that feeds on only one species of plant which can grow in only one type of geologic formation in a narrow range of altitude to a species that feeds on many plants which grow on many geologic formations in a wide range of altitude.

A good example of a butterfly restricted to one rock type is *Euphydryas editha* in California (Johnson et al. 1968) which is usually restricted to serpentine outcrops.

We can link only a few of the butterflies in the Pueblo area closely to the chemistry of the rocks or soil. They are all mainly low altitude species: *Chlosyne leanira* — foodplant *Castilleja integra* which at least at altitudes of 5000-7000 ft. grows on limestone or on gypsum deposits or calcareous soils developed on either surficial deposits or on bedrock; *Pieris chloridice (beckerii)* — foodplants Cruciferae and Capparidaceae mostly growing on gypsiferous shale or claystone; *Phycoides picta* — foodplant *Aster* growing on gypsiferous shale or on alkaline soils; *Pholisora alpheus — foodplant Atriplex canescens* which grows on alkaline soils; *Pholisora mejicana* — foodplant *Amaranthus* species growing on alkaline soils. Probably other butterflies do use foodplants that are restricted to certain soils or rocks, but confirmation of this would require a special study.

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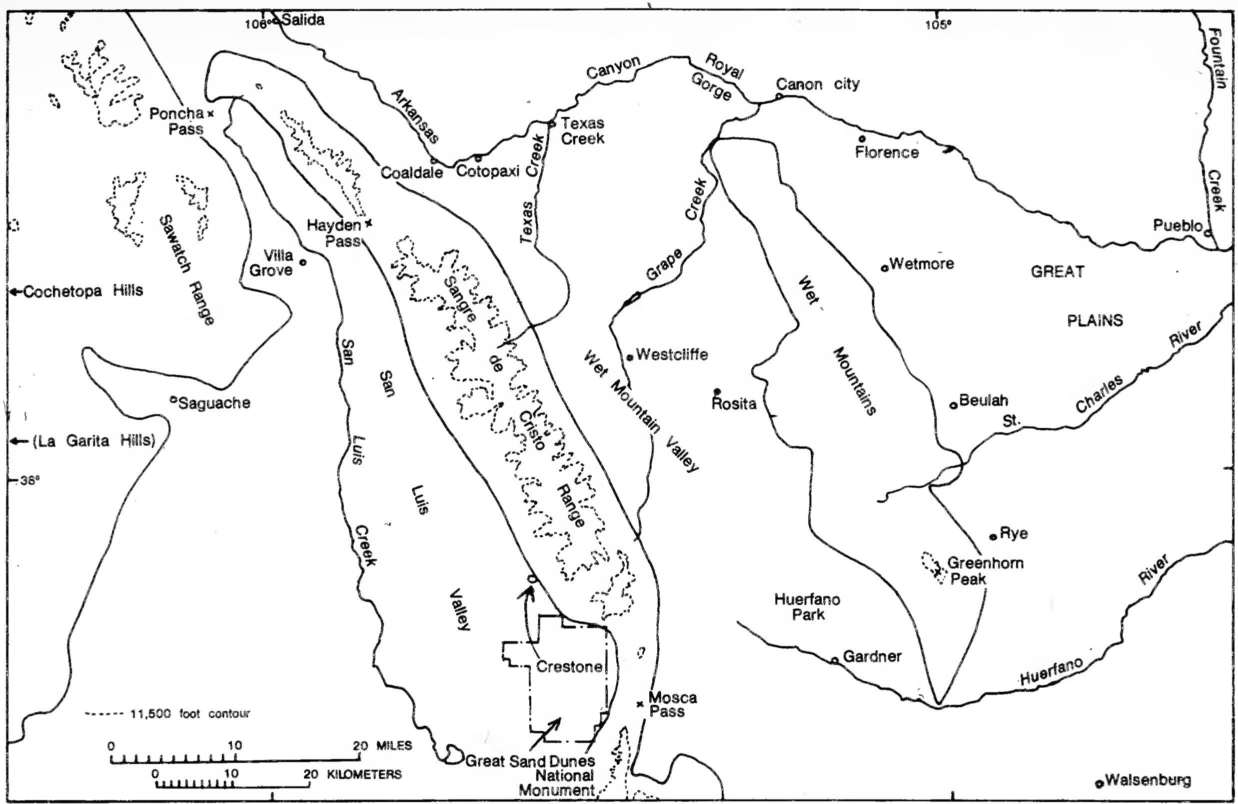

Fig. 1. Outline Map derived from the Southern half of the Pueblo Quadrangle (1:250,000) giving names of the physical features and some towns.

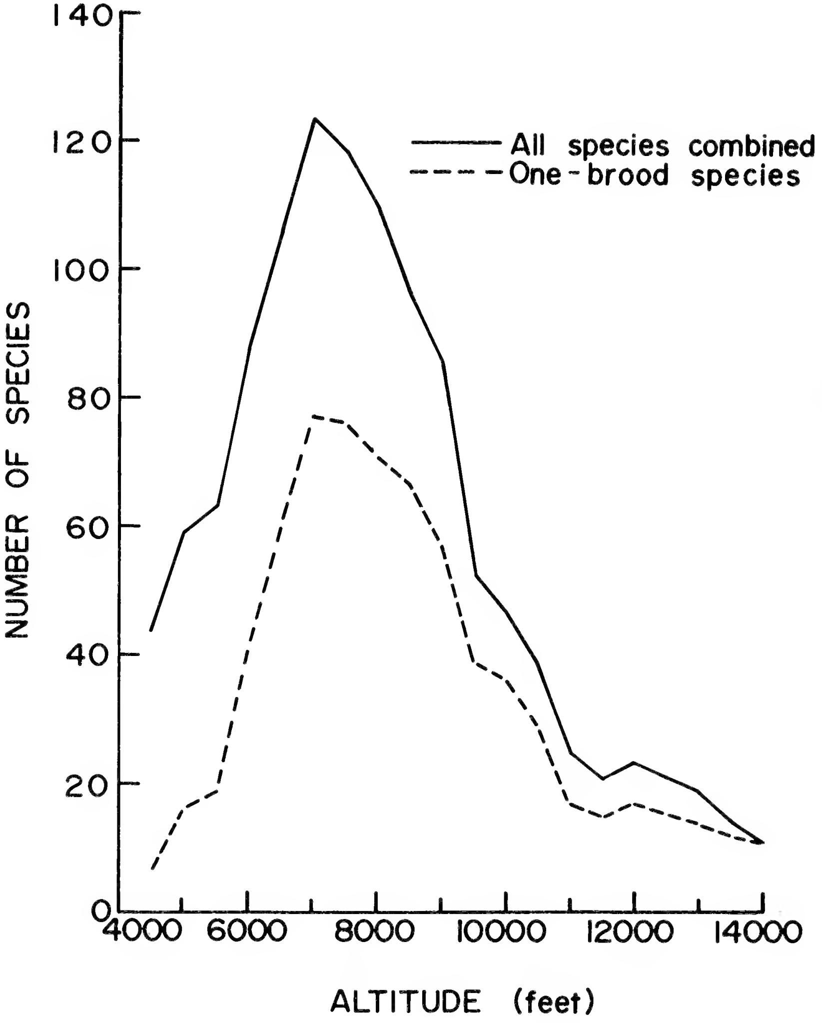

Fig. 2. Number of native species occurring at each altitude.

Table 1. Distribution of the 160 native species within the Pueblo area.

Group 1	Widespread	
	40	species occur throughout the area (although only 9 of these occur at all elevations and all 9 disperse widely except that *Nymphalis milberti* and *Plebejus acmon* apparently breed above timberline).
	47	species occur throughout the mountains (only 4 also occur in the alpine zone).
Group 2	More restricted in distribution apparently due to limited habitat or altitude requirements.	
	15	occur at middle altitudes throughout the mountains
	6	occur in subalpine areas of all three ranges
	6	only in alpine areas
	6	only on the plains
	6	only in the Wet Mountain foothills
	3	plains, Arkansas Canyon, and San Luis Valley (*Pieris chloridice, Pholisora alpheus, Megathymus streckeri*)
	1	Wet Mountain Valley and San Luis Valley (*Boloria selene*)
	2	Arkansas Canyon and San Luis Valley (*Chlosyne acastus, Polites sabuleti*)
	2	Arkansas Canyon, Wet Mountain Valley, and San Luis Valley (*Euphilotes rita, Lycaena heteronea*)
	1	plains and San Luis Valley (*Limenitis archippus*)
	3	plains, foothills, and Arkansas Canyon (*Euchloe olympia, Erynnis afranius, Atalopedes campestris*)
	2	plains, Arkansas Canyon (*Atrytonopsis vierecki, Phyciodes picta*)
	2	plains, foothills (*Asterocampa celtis, Everes comyntas*)
	4	foothills, Arkansas Canyon (*Pholisora mejicanus, Oarisma edwardsii, Amblyscirtes aenus, A. vialis*)
Group 3	Species which occur only on one side of the Sangre de Cristo Mountains and are absent on the other side in apparently suitable habitats.	
	2	plains and Wet Mountain Valley (*Lycaena hyllus, Brephidium exilus*)
	4	throughout the area except the San Luis Valley (*Chlosyne gorgone, C. leanira, Cercyonis pegala, Amblyscirtes oslari*
	3	Wet Mountain foothills, Arkansas Canyon, Wet Mountain Valley (*Satyrium liparops, Thorybes pylades, Erynnis horatius*)
	1	plains, foothills, Wet Mountain Valley (*Chlosyne nycteis*)
	4	San Luis Valley only (*Cercyonis meadii, Euphilotes spaldingi, Polites sonora, Oeneis alberta*)

Table 2. Distribution of the 247 butterfly species of Colorado.

1. 30 species are strays from the south which usually appear on the eastern plains.

2. 54 are widely distributed in the state.

3. 105 occur in the mountains on both slopes of the Continental Divide (9 are primarily subalpine species, and 8 are primarily alpine species).
    a. 69 occur throughout the mountains in suitable habitats
    b. 9 occur throughout the mountains and extend out onto the plains in some areas.
    c. 8 occur only in the northern mountains
    d. 3 occur only in the southern mountains
    e. 1 occurs throughout the mountains except for the Front Range
    f. 7 occur mostly throughout the mountains except for the Wet and Sangre de Cristo Mountains and San Luis Valley
    g. 2 occur throughout the mountains except for northwestern mountains.
    h. 3 occur in parts of the alpine areas of the state but are continuously distributed there
    i. 3 occur in widely disjunct areas of the mountains

4. 38 occur only east of the Continental Divide.

    a. 7 occur only in mountains
    b. 5 occur both in the mountains and the plains
    c. 13 occur mostly on the plains where they are widespread
    d. 5 occur only in the northeastern plains
    e. 4 occur only in the southeastern plains
    f. 4 occur only on the eastern plains near Kansas

5. 17 occur only west of the Continental Divide.
    a. 1 occurs throughout the mountains
    b. 4 occur only in the northwestern mountains
    c. 1 occurs only in the southwestern mountains
    d. 4 occur only in the southwestern corner of the state
    e. 7 occur only on the western edge of the state near Utah

6. 3 species occur widespread across the southern part of the state.

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The Biology of *Plebejus (Icaricia) shasta* in the Western United States (Lycaenidae)

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Abstract: 1. The habitat, foodplants, and life history of *Plebejus (Icaricia) shasta* are described, based on field observations of a number of populations in the western United States. 2. 13 foodplant species are recorded for *P. shasta;* four genera are represented and all are in the family Fabaceae.

Introduction

We report here the results of our field studies and museum research on *Plebejus (Icaricia) shasta* (Edwards) over a ten year period. This species first engaged our interest during the summer of 1967 when we made several observations on its habitats and foodplants. Following this, we did extensive field work in 1968, 1969, and 1970. From 1971 to 1977, we gathered records from various individuals and institutions and did further field studies, to help determine distribution, flight period, and patterns of geographic variation.

Taxonomy and Distribution

Ferris (1976) revised the taxonomy of *P. shasta* and concluded that three subspecific names were sufficient to apply to all known populations. The California and Oregon populations fell under nominate *shasta, pitkinensis* Ferris referred to arctic-alpine populations in Colorado, and *minnehaha* Scudder was used for the remaining populations from the Great Basin to the western prairie region. *P. s. comstocki* Fox was sunk as a synonym of nominate *shasta,* and *P. s. browni* Ferris was relegated to synonymy under *minnehaha.*

Although we are in general agreement with most of Ferris's concept of the subspeciation of *P. shasta,* we would make several changes in this scheme. We see the name *minnehaha* serving primarily as a "waste-basket" category for a rather diverse array of geographically isolated populations, to be used only until more detailed studies can be made. Numerical taxonomy may prove to be the best means of sorting these out. Also, phenotypically and biologically, certain populations that Ferris included with nominate *shasta* seem to have a closer affinity with the Great Basin populations. These are the Oregon populations and the California populations in the White Mountains (Inyo and Mono counties) and in Modoc and Lassen counties; these we would temporarily "lump" with *minnehaha*. We have not personally examined specimens from the Mt. Shasta region and cannot comment on their affinities.

The Wyoming specimens from the slopes of Medicine Bow Peak, 11,500', Carbon Co., are included with *minnehaha* by Ferris. Biologically and phenotypically, we feel that these are much closer to *pitkinensis*. The single female of this population that we have examined shows the slate-blue-gray upperside typical of the Colorado specimens of *pitkinensis*.

Specimens from the Spring Range, Clark County, Nevada, are particularly distinctive from the three described subspecies; this new subspecies is being intensively studied by George Austin of Las Vegas, Nevada. He will publish the results of his studies in a future paper.

We agree with Ferris that records for *shasta* from Alaska, British Columbia, and Washington are highly questionable and need confirmation before the species can be stated to exist in these regions. A single male in the Los Angeles County Museum labelled "Tehachapi Mts., Kern Co., Calif", is also doubtful as no other specimens are known from that relatively well-collected mountain range.

Habitat

Although *P. shasta* is found over a wide altitudinal range (1,200 to 13,000 feet elevation), its immediate habitat exhibits a number of common features. Typically, it occurs on open, exposed, sunny, gravelly-soiled and well-drained flats, slopes, hilltops, or ridges. These areas are often free of winter snow relatively early in the spring. Although the winter snowfall may be substantial (as at Donner Pass, Caifornia), by the time *P. shasta* adults are in flight, the ground is usually quite dry due to the combination of good drainage and early snowmelt from a favorable slope exposure.

At most elevations below approximately 11,500', the associated plant community is Sagebrush Scrub (Munz, 1959). At the highest elevations, the species flies over arctic-alpine fell-fields. Regardless of elevation, the associated vegetation is usually scrubby, low-growing, and relatively sparse. Some of the plants in *P. shasta* habitats in the Sierra Nevada are prostrate *Eriogonum* species, *Castilleja nana* Eastw., *Penstemon heterodoxus* Gray, and *Erigeron pygmaeus* (Gray) Greene. In the Great Basin ranges, some of the most commonly associated plants are *Artemisia tridentata* Nutt., dwarf *Castilleja* species, and *Pinus aristata* Engelm. In the Rocky Mountain region, Ferris (1976) notes the associated plants to be *Sedum* species and *Eriogonum* species in addition to sagebrush.

Foodplants

We recorded 13 species of Fabaceae as foodplants for *P. shasta.* These plants are listed in the Table, and are documented in the Appendix in accordance with a method we have previously described and used (Shields et al, 1969).

Although four genera are represented, all foodplants, with one exception, have a remarkably similar growth habit. They are perennials with long taproots, growing in a prostrate manner or forming mats on the ground. This is an adaptation to the exposed areas where these plants grow, where high winds are frequent and occasional heavy winter snows produce an enormous weight on the underlying vegetation.

The majority of plants used are in the genus *Astragalus.* This is a very large genus within the territory covered by the range of *P. shasta,* with over 100 species represented (Barneby, 1964). Undoubtedly more foodplants in this genus will be recorded in future field work. We record one species of *Oxytropis,* a genus very closely related to *Astragalus.* The three *Trifolium* species used by *P. shasta* are adapted to dry, exposed slopes, unlike many members of this genus which prefer moist meadows.

Of the three *Lupinus* species we recorded, two are mat-formers while the third, *L. arbustus,* grows as a small herbaceous bush. We suspect that *L. arbustus* is not a regularly used host, and that this plant and certain other fabaceous species may be used occasionally if they are growing in close proximity to commonly used *shasta* foodplants. In the case of *L. arbustus,* we searched numerous individuals of this species but found only a single larva of *P. shasta* feeding on it. On nearby plants of *Astragalus whitneyi, shasta* larvae were relatively easy to locate. Similarly, when we observed ovipositing females in this same locality (Donner Pass) at a later date, *Astragalus* was repeatedly visited while *L. arbustus* was ignored. In view of the large number of plant species used by *shasta,* and hence a relatively broad variety of biochemical stimuli tolerated by ovipositing females, it is not surprising that non-prostrate fabaceous species are sometimes used. This suggests that ovipositing females are responding to the visual stimulus of a prostrate growth habit in addition to biochemical stimuli.

Life History

The females we observed would hover about and land repeatedly on the foodplant, and then walk over the plant for several seconds to minutes before ovipositing. Oviposition did not take place on any particular part of the plant. Ova were placed on leaf surfaces, petioles, stems, and seed pods. Occasionally, an ovum would be deposited on ground litter near the base of the plant. We found a number of hatched eggshells adjacent to newly laid eggs, indicating that the ova do not overwinter. Diapause is likely passed as a partly-grown larva, similar to *Plebejus icarioides* (Boisd.) (Comstock & Dammers, 1935).

Soon after snowmelt in mid-June, we found nearly mature, post-diapause larvae at two localities in the Sierra Nevada. These larvae were found feeding on the flowers and young leaves of the foodplant, or else resting in ground litter near the bases of the plants. Unfortunately, due to other pressing matters at the time that the larvae were collected, we were unable to make detailed notes on larval morphology and coloration. A photograph of one of these larvae by Edward Ross is shown in Figure 1. The ground color of the mature larva is a dirty white or cream with prominent dark brown chevrons when viewed dorsally.

Pupation probably takes place in ground litter near the caudex of the foodplant. In the rearing jars, pupation took place under foodplant litter at the bottoms of the containers. Emergence of adults occurred about two weeks after pupation, always in the early morning hours. Pupal morphology is similar to that of *Plebejus (Icaricia) acmon* (Westw. & Hew.) and *P. (I.) icarioides* (see Comstock & Dammers, 1935). The wing cases are pale green, with the body light tan to pale greenish-tan.

Four species of ants were noted to "tend" the post-diapause larvae. At Donner Pass, Placer Co., Calif., *Formica fusca* Linne and *F. neogagates* Em. were the associated ants. Both *Formica densiventris* Vier. and *F. oreas* Whlr. were observed to tend larvae at Ebbetts Pass, Alpine Co., Calif.

Flight Period

Most adults have been taken during the months of July and August, although June captures are not uncommon at the lower elevations. Date of emergence depends on a number of factors, including elevation, snowpack, slope exposure, and time of snowmelt. Considerable spread is possible in a given locality due to local variations in exposure and time of snowmelt. The earliest record we have is June 9 at 5100 feet elevation in Wyoming. The latest record is September 6 at 12,000 feet elevation in California.

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Appendix

Collection and Foodplant Records

In the following list of records, collectors' names are given in parentheses. Collecion of deposition is that of the collector(s) unless otherwise designated by the initials of another collector or institution (see Acknowledgements for key to initials). Foodplant records are reported in accordance with a method we have previously described (Shields et al, 1969). All foodplant records are observations by the authors unless otherwise noted.

P. shasta shasta

CALIFORNIA. *Alpine Co.:* Carson Pass, rocky ridge, VII-6-61, "1" (N. La Due); Carson Pass, Winnemucca Lake, 9000', VIII-24-64, 1♂ 1♀ (D.L. Bauer); Carson Pass, slope of Red Lake Pk., 9000', VIII-17-64, 1♀ (D.L. Bauer); ridgetop E. of Hwy. 88 at Carson Spur, 8000-9000', VII-18-71, 5♂ 1♀ (R. Wells); Ebbetts Pass, 8730', VIII-7-69, open gravelly hilltop, ♀ oviposited at 11:20 PST on underside of leaflet, another at 11:30 PST on upperside of leaflet of *Astragalus purshii* Dougl. (*J.F. Emmel #211,* CAS); Ebbetts Pass, on slope 0.2 air mile SSE of Ebbetts Peak, 8750', VI-17-70, open gravelly slope, 12 larvae, 4th-5th instar, at base of plants or feeding on flowers of *Astragalus purshii* Dougl. (*J.F. Emmel #306,* CAS); Ebbetts Pass, 8700-9100', VII-18-54, 2♂ (P. Opler); VI-30-60, 1♀ (J. Powell, CIS); VII-26-65 (D. L. Bauer); VIII-1-70, 7♂ (R. Wells); VIII-8-71, "3" (J. Mori & O. Shields); NW above Ebbetts Pass, VII-20-72, "1" (R. F. Denno, R. Rust, O. Shields); Monitor Pass, 8300', VII-16-72, 3♂ 1♀ (R. Wells); VII-23-64 (D. L. Bauer); 1.4 mi. N. Monitor Pass, Hwy. 89, 7950', VII-2-74, 1♀ (E. M. Perkins & O. Shields). *Amador Co.:* Carson Spur, nr. Silver Lake, VII-18-57, 8♂; VIII-5-57, 1♂ 1♀;VII-18-58, 10♂; VII-24-58, 2♂ 4♀; VI-30-59, 3♂ 1♀;VII-8-59, 1♂ 1♀; VI-27 & 28-60, 29♂ 2♀; VII-6-61, 1♂ (all N. La Due); Carson Spur, VII-18-71, 5♂ (J. Brock); Silver Lake, VII-20-41, 1♂ (UCD); Tragedy Springs, 8000', just W. of Silver Lake on old Hwy. 88, VII-6-61, 2♂ (N. La Due). *El Dorado Co.:* Job's Sister Pk., 9000', SE end Lake Tahoe, VIII-4-63 (D. L. Bauer); trail between SW end Fallen Leaf Lake and summit Mt. Tallac, 6300-9700', VIII-28-76, "1" (O. Shields & S. Sims). *Fresno Co.:* Kaiser Crest, VII-21-73 (In: News Lepid. Soc. 1974, No. 2, 19 pp., Season Summary for 1973); Mono Pass, IX-6-47, 1♀ (C. D. MacNeill, CIS). *Fresno-Inyo Co. line:* Piute Pass, 11,400', VIII-11-63, 1♂ (O. Shields). *Kern Co.:* Tehachapi Mts., VIII-22-37, 1♂ ("pres. by W. A. Evans collector", LACM). *Mariposa Co.:* Boundary Hill, Research Reserve Area, Yosemite Nat'l Park, VII-20-70, 1♀ (R. P. Allen, UCD). *Mono Co.:* Carnegie Exp. Gardens, 10,000', Slate Creek Valley, VIII-8- to 13-64, "a few" (O. Shields); W. end of Dana Plateau, 11,000', above Tioga Pass, VIII-8-69, open gravelly ground, ♀ oviposited at 2:20 PST on leaf near base of *Lupinus lyallii* Gray (*J. F. Emmel # 215,* CAS); just over E. side of Donahue Pass, VIII-4 to 6-59, "common, 50 taken" (O. Shields); trail to Upper Gaylor Lake, Tioga Pass, VIII-26-56, 3♂ 2♀ (R. Langston); VII-9-61, 1♂; VII-30-61, 3♂ (both S. Mattoon); Glacier Canyon, ca 11,000-11,300', N. slope Mt. Dana, VII-4-64, 2♂ (O. Shields); Leavitt Peak, 11,000', Sonora Pass, VIII-9-64, 1♀ (D. L. Bauer); Mammoth Crest, VII-18 & 21-52, 4♂ 1♀ (J. Powell, CIS); Mammoth Rock, VII-29-52, 12♂ 6♀ (J. Powell & M. J. McKenney, CIS); Minaret Vista (ridge), Hwy. 203, W. of Mammoth Mtn, 9265', VII-6-74, 3♂ (E. Perkins & O. Shields); 1.2 air miles S. of Bodie, Bodie Hills, 8480', VII-26-74, several females showed pre-oviposition behavior toward *Lupinus breweri* Gray var. *bryoides* C. P. Sm. in Jeps. (*J. F. Emmel #526,* RSABG); Mt. Dana, VIII-16-53, 4♂ (n. La Due); Saddlebag Lake, VII-21-54, 1♂ (J. Powell, CIS); Tioga Crest, VI-21-52, 1♀ (J. Powell, CIS); Tioga Pass, 9900-10,000', VII-14-58, 4♂; VII-30-64, 3♂ 4♀; VII-24-66, "8"; VII-26-72, 1♂ 3♀ (all O. Shields); NW above Tioga Pass, VIII-22-65, 1♂ 2♀ (O. Shields); W. above Tioga Pass, VIII-3-58, 1♂ (N. La Due); VIII-20-58, 2♂ 2♀; VIII-10-63, 5♂ (both O. Shields). *Nevada Co.:* Sagehen Crk., VII-15-66, 1♂ (UCD). *Placer Co.:* N. slope of Donner Peak, 7600', VII-25-68, on exposed dry gravelly slope, 3♀ observed to oviposit on plants, mainly on leaves, of *Astragalus whitneyi* Gray (*J. F. Emmel #100,* DHSU); slope between Donner Peak & Donner Pass, 7400', VI-15-69, on open gravelly slope, six 5th instar larvae feeding on leaves and flowers, some hiding at base of plant, of *Astragalus whitneyi* Gray (*J. F. Emmel #167,* CAS); N. slope of Mt. Judah, VII-6-63, 2♂ 3♀; VIII-21-67, 1♂ 1♀ (both N. La Due); north peak of Mt. Judah, 8100-8200', S. above Donner Pass, VI-15-69, on open gravelly slope, one 5th instar larva in litter at base of *Lupinus arbustus* Dougl. (*J. F. Emmel #168,* CAS) (larva reared to pupa on same plant). *Siskiyou Co.:* Methodist Camp Meadow, Castle Lake (S. Mattoon); W. slope Mt. Eddy, SW of Weed, VII-1-74, "large series" (S. Mattoon). *Tulare Co.:* Shepherd Pass trail, divide between Wright Lakes & Tyndall Creek, 11,200-12,200', VII-27-66 (S. Ellis & S. Johnson). *Tuolumne Co.:* above Upper Gaylor Lake, 11,200', VIII-3-68, on open rocky slope, 2♀ oviposited on stem and leaf underside of *Lupinus lyallii* Gray (*J. F. Emmel #104,* DHSU); Blue Canyon, Sonora Pass, VIII-30-60, 1♀ (J. Powell, CIS); meadows & slopes by Helen Lake, S. of Tioga Pass, VII-18-58, 5♂ (O. Shields); Lunch Mdw., nr. Emigrant Basin, VIII-15-54, 1♂ 1♀ (P. Opler); N. of Sonora Pass, VII-5-59, 1♂ (N. La Due); Sonora Peak, VIII-10-57, 1♀ (J. Powell, CIS); above Upper Gaylor Lake, ca. 11,000', VI-19-58, 2♂ (O. Shields). *Tuolumne-Mono Co. line:* Sonora Pass, VII-8-61, 2♂ (S. Mattoon); VIII-1-52, 1♂ 1♀; VIII-5-58, 2♂; VII-7-59, 2♂ (all N. La Due); VII-3-59, 5♂ 2♀; VII-18-59, 4♂; VII-2-66, 1♂ 1♀ (all P. Opler); VIII-21-59, 2♂ (J. Powell, CIS); VII-31-64, 4♂ 1♀ (O. Shields); VII-9-64, 1♂ 1♀; VIII-9-67 (both D. Bauer); VIII-7-71, "7" (J. Mori & O. Shields); IX-5-71, 3♂ 2♀ (R. Wells); VIII-12-73, 2♂ (S. Sims).

NEVADA. *Ormsby Co.:* Snow Valley Pk., 9274', Carson Range, VII-27-64, 1♂ 1♀ (D. Bauer). *Washoe Co.:* Lake Tahoe (Glen Alpine & Mt. Rose area), VII-26-50, 1♂ 1♀ (D. Bauer); Mt. Rose summit, 8500', Carson Range, VII-29-64, 1♂ (D. Bauer); Tamarack Lake, Mt. Rose, VII-29-64 (D. Bauer).

P. shasta minnehaha and Great Basin populations

CANADA: ALBERTA. Red Deer River, Gleichen, VII-1, 5, 6-05, 2♂ 1♀ (F. Wolley Dod, LACM).

UNITED STATES. CALIFORNIA. *Inyo Co.:* Bristlecone Pine Nat. Mon. at Hdq., VII-22-68, 2♂ (R. Wells); 0.5 air mile SE of Goat Spring, 4 mi. S. of County Line Hill, White Mts., 10,400', VII-6-68, on open gravelly ground. 3 ova on plants, underside of laf and on stem, and ♀ oviposition behavior toward these plants, on *Astragalus kentrophyta* Gray var. *implexus* (Canby) Barneby (*J.F. Emmel #111,* DHSU); same locality & date, ♀ oviposited on leaf underside of *Trifolium monoense* Greene (*J. F. Emmel #110,* DHSU); White Mts., VIII-3-72, "common" (J. Brock & R. Wells). *Lassen Co.:* Susan River nr. Bridge Creek Camp, VII-8-49, 1♂ (R. Langston); 5 mi. N. Westwood, VII-2-61, 1♂ (O. Shields). *Modoc Co.:* NW slope of Mt. Bidwell, 7900', Warner Mts., VII-16-68, on open ground, sagebrush, several ♀ showed pre-oviposition behavior toward *Astragalus purshii* Dougl. (*J.F. Emmel #84,* DHSU). *Mono Co.:* Crooked Creek Lab., 10,150', White Mts., 3 air mi. N. of Inyo Co. line, VI-26-61, 3♂ 1♀ (J. Powell, CIS: S. Buckett, UCD); VII-20-61, 5♂ 3♀ (J. Powell, CIS); Mt. Bancroft, 12,500', White Mts., VII-11-61, 1♂ (J. S. Buckett, UCD); Mt. Barcroft Lab., 12,500', White Mts., 9 air mi. N. Inyo Co. line, VII-21-61, 1♀ (J. Powell, CIS); Sheep Mt., 11,200', White Mts., VII-6-61, 4♂ 3♀ (J. Powell, CIS).

COLORADO. *Moffat Co.:* nr. Diamond Peak, 9200', VII-8-72 (J. Scott).

IDAHO. *Bear Lake Co.:* M-Hill, Montpelier, VII-14-29, 2♂ (W. J. Gertsch, BYU). *Lemhi Co.:* N. side of Gunsight Peak, 9200', Lemhi Range, VII-31-72 (S. Ellis & L. Thompson).

MONTANA. *Fergus Co.:* 2 mi. S. of summit on Heath-Slayton road, 6000', Big Snowy Mts., VI-15-69, 1♀ (J. Shepard). *Golden Valley Co.:* 8 mi. S. of summit of Heath-Slayton road, 4800', Big Snowy Mts., VI-15-69, 3♂ 1♀ (J. Shepard). *Meagher Co.:* Martindale, VI-18-00, 2♂ (C.J. Paine, MCZ).

NEBRASKA. *Sioux Co.:* canyon region N. of Harrison, VII-14-17, 1♂ 1♀ (R.A. Leussler, AMNH).

NEVADA. *Clark Co.:* Kyle Canyon, 8500-9000', VII-25 & 27-65 (A. Austin); Lee Canyon, 8250-8800', VII-21-63 (A. Austin); Willow Creek, 6000-8000', Charleston Range, VII-15-28-28, 15♂ 19♀ (J. Gunder, AMNH). *Douglas Co.:* Pine Nut Mts. (D. Bauer). *Elko Co.:* ridge 0.5 air mile due N. of Angel Lake, 8700', East Humboldt Range, VII-26-69, gravelly open area, ♀ oviposited at 1:30 PST on leaf upperside of *Astragalus calycosus* Torr. var. *mancus* (Rydb.) Barneby (*J.F. Emmel #197,* CAS); Angel Lake Cpgd., VII-16-73 "in numbers on gravelly ridges" (D. Eff, RL); peaks above Angel Lake, East Humboldt Range, VII-20-73, 2♂ (S. Sims); East Humboldt Range, high ridgecrests, VIII-5-71, "substantial series" (S. Mattoon); trail from Dollar Lake to Liberty Pass, S. end of Lamoille Cyn., 9600-10, 450', Ruby Mts., VII-25-69, 7♂ 2♀ (J. Emmel & O. Shields); ridge ⅜ air mile NW of Island Lake, 10,800-11,200', above Lamoille Cyn., Ruby Mts., VIII-8-67, 4♂ (J. Emmel, S. Ellis, O. Shields); slope 0.5 air mile S. of Bonanza Gulch, Jarbidge Mts., 8000-8500', VI-22-69, 27♂ 5♀ (J. Emmel & O. Shields); Bear Creek Summit, 8488', Jarbidge Mts., VII-24-69, 1♂ (J. Emmel & O. Shields); north slope of peak 2 air miles NE of Spruce Mtn. peak, 8800-9200', VII-28-69, 1♂ (J. Emmel & O. Shields). *Humboldt Co.:* summit of Buckskin Mtn., 8740', Santa Rosa Range, VIII-11-67, several females showed pre-oviposition behavior toward *Astragalus newberryi* Torr. (*J.F. Emmel #35,* DHSU); VII-20-69, 1♂ (J. Emmel & O. Shields); Hinkey Summit, 8000', Santa Rosa Mts., VII-14-64, 1♂ (D. Bauer); 14-16 mi. N. Paradise Valley, 7100-7867', VII-10-66, 1♂ 2♀ (F., P., & M. Rindge, AMNH); road to Blue Lake, ca. 8000', Pine Forest Range, VIII-1-71, 9♂ 30♀ (S. Mattoon); Sonoma Range, ridge between Water Cyn. & Thomas Cyn., 8000', VII-18-77, 1♀ (J. Emmel). *Lander Co.:* Bunker Hill, 11,400', Toiyabe Range, VIII-4-69, on gravelly slope near top of ridge, ♀ oviposited at11:45 PST on underside of petiole of *Astragalus platytropis* Gray (*J.F. Emmel #208,* CAS); ridge to the WSW of Bunker Hill, 10,000-10,400', Toiyabe Range, VII-4-69, 5♂ 2♀ (J. Emmel & O. Shields); Bunker Hill and ridge to the SW, 11,000-11,474', Toiyabe Range, VII-4-69, 6♂ (J. Emmel & O. Shields); ridge 1.2 air miles NNE of highest peak of Bunker Hill, 10,000-10,400', Toiyabe Range, VIII-11-68, 1♂ (J. Emmel & O. Shields). *Mineral Co.:* Big Indian Mt., 10,000', Wassuk Range, VIII-3-64, 3♂ 4♀ (D. Bauer); Collins Canyon, 7800-9000', Wassuk Range, VIII-3-64, 1♂ (D. Bauer); Cory Peak, 10,500', VIII-3-64, 1♂ (D. Bauer). *Nye Co.:* toward upper end of Jett Canyon (3-4 mi. up canyon), Toiyabe Range, VII-9-71, 1♂ (O. Shields); E. side of alpine plateau of Mt.

Jefferson, 11,000', Toquima Range, VIII-4-67, ♀ oviposited on *Astragalus calycosus* Torr. (*J.F. Emmel #28,* DHSU); Pine Creek Cyn. Cpgd., 8100', E. side Toquima Range, VIII-4-67, 1♂ (J. Emmel, S. Ellis, O. Shields). *White Pine Co.:* Upper Lehman Creek, 14 mi. W. of Baker, 9800', VIII-4-66, 1♂ 1♀ (F., P., & M. Rindge, AMNH); Wheeler Peak, 10,000', VII-26-69, 5♂ 1♀ (C. Callaghn); trail from Wheeler Peak Campground to ridge above Stella Lake, 11,000', N. end of Snake Range, VII-30-69, on rocky ridgetop, gravelly soil, ♀ oviposited at 9:00 PST on leaf underside of *Trifolium gymnocarpum* Nutt. (*J.F. Emmel #200,* CAS); same locality & date, ♀ oviposited at 9:35 PST on underside of petiole of *Oxytropis parryi* A. Gray *(J.F. Emmel #201, CAS);* same locality, VIII-1-67, 1♂ (J. Emmel, O. Shields, S. Ellis)

OREGON. *Deschutes Co.:* Davis Lake, 4395', VII-22-34 (Dornfeld records); Little Cultus Lake & Cultus Creek, 4500', VII-4-63 (E.J. Newcomer); Pringle Falls, 4200', VII-23-60 (E.J. Newcomer); Snow Creek, 4600', VIII-4-63 (E.J. Newcomer). *Harney Co.:* Fish Lake, 7400', VIII-11-61 (E. J. Dornfeld); head of Little Blitzen Cr., 9300', VIII-8-64 (C. R. Crowe, Dornfeld records); Steens Mts., 9000', VIII-10-68 (E. J. Newcomer); Steens Mt. summit, 9500', VII-28-68 (C. W. Nelson, Dornfeld records); nr. summit of Steens Mts., 9500', VIII-13-67, 1♂ 1♀ (S. Mattoon); Steens Mts., ca. 7000', VII-25-36 (Dornfeld records). *Klamath Co.:* Beaver Marsh, VII-16-64, VII-16-64 6♂ 2♀ (J. Scott); ca. 5-10 mi. E. Beaver Marsh, ca. 4700', VI-14-61, 9♂ "on a lupine" (O. Shields); ca. 5 air mi. NE Chemult, along road to Walker Mtn. Lookout, Walker Rim, VII-9-70, 2♂ (S. Dvorak & O. Shields); 4 mi. SE of Crescent, ca. 4500', VII-15-61, 5♂ 1♀ (O. Shields); Diamond Lake, VII-14-33, 1♂ (UCD); Gilchrist, 4500', VIII-7-60, VII-28-62, VIII-14-63 (all E. J. Dornfeld); Skookum Meadow (Walker Rim), 5200', VI-23-61 (E. J. Newcomer). *Lake Co.:* Cannon Well, 5400', VII-30-61 (E. J. Newcomer); Drake Peak, 8000', VIII-3-63 (E. J. Newcomer); 3 mi. S. of Silver Lake, ca. 4800', VII-17-55 (R. J. Albright, Dornfeld records).

UTAH. *Box Elder Co.:* Clear Creek Canyon, 5600', Raft River Mts., VII-23 & 24-63, 1♂ 3♀; VII-13-66, 3♀ (both K. Tidwell); Holstein Ranger Station, 6500', VII-23-63, 2♀ (K. Tidwell). *Sanpete Co.:* 17 mi. E. Mayfield, 10,200', VIII-1-58, 1♂ (F., P., & J. Rindge, AMNH); Wasatch Plateau near Mt. Sanpete, 11,000', E. of Ephraim, VII-31-67, several females showed pre-oviposition behavior toward *Astragalus kentrophyta* Gray var. *elatus* Wats. (*J.F. Emmel #26,* DHSU); *Tooele Co.:* Deep Creek Mts., 9000', VII-24-67, 1♂ (C. Callaghan). *Uintah Co.:* Blue Mountain Plateau, vic. Relay Station, 7800', Dinosaur Nat. Mon., VI-22-68, 2♂ (S. Ellis); Dinosaur Nat. Mon., VI-18-66, 1♂ 3♀ (C. Callaghan); Iron Springs Camp, 25 mi. N. Vernal, 8700', VII-20-63, 1♀ (F., P., & M. Rindge, AMNH). *Wayne Co.:* Cathedral Valley Rd., 2.5 mi. E. of intersection with Elkhorn Campground Rd., 8400', VI-19-72 (S. Ellis & L. Thompson); Cathedral Valley Rd., 1 mi E. of intersection with Elkhorn Cpgd. Rd., NE side of 1000 Lake Mtn., 8800', VI-19-72 (S. Ellis & L. Thompson).

WYOMING. *Albany Co.:* Telephone Creek, 8900', VII-18-62, 1♀ (J. K. Windsor, LACM); 2 mi. E. Laramie, 7200', VII-16 & 27-69 (C. D. Ferris, DG); Sybille Canyon, 2 mi. E. of Morton Pass on Wyo. Hwy. 34, 6700', VII-4, 10-11-66, VII-23-67, VII-12-69 (all D. Groothuis & R. Hardesty). *Carbon Co.:* N. of Riverside, 7000', VII-11-52, 2♂ 1♀ (V. Nabokov, MCZ). *Converse Co.:* ½ mile E. Douglas, 5100', VI-25-67, VII-9-67, VI-9, 17-69 (D. Groothuis & R. Hardesty); North Horseshoe

Creek, nr. Esterbrook, 6500', VII-9-67 (D. Groothuis & R. Hardesty). *Fremont Co.:* Dubois, 6500, VII-52, 2♂ 9♀ (V. Nabokov, MCZ). *Yellowstone National Park:* Sylvan Pass, VII-24-27, 2♂ (J. Comstock, LACM).

P. shasta pitkinensis

COLORADO. *Boulder Co.:* Arapahoe Pass Trail, VII-6-53, 1♂, IX-1-47, 1♂ 1♀ (D. Eff,LACM); Niwot Ridge, VII-29-51, 1♂ 1♀ (D. Eff, LACM); Brainerd Lake, VII-27-47, 1♂ 1♀ (D. Eff, DB); Lefthand Park, VII-27-47, 1♂ 1♀ (D. Eff, DB). *Chaffee Co.:* Cottonwood Pass, VII-17-59, 1♂, VIII-8-61, 4♀ (R. Jae, NL, CC); Monarch Pass, VII-6-61 (J. Scott). *Clear Creek Co.:* Loveland Pass, VII-16-60; VII-28-72; VII-26-73 (all J. Scott). Mt. Evans, VII-7-60, 1♂ (LACM); Mt. Goliath, VIII-8-59, 2♂ 1♀ (R. Buchmiller, PO). *Clear Creek - Grand Co. line:* Berthoud Pass-Vasquez Peak, 11,314-12,927', VII-29-67, 14♂ 1♀ (F., P., & M. Rindge, AMNH). *Custer Co.:* Baldy Peak, 12,500', VII-29-70, 2♀ oviposited on *Trifolium dasyphyllum* T. & G. (J. Scott); Hermit Pass, 12,000-13,000', VII-23-70, VIII-1-71, oviposition on *Trifolium dasyphyllum* T. & G. (J. Scott); Rainbow Lake, VIII-13-67 (M. Howard, JS); Silver Lake, ca. 12,300', VIII-16-68 (J. Scott). *Fremont Co.:* Bear Creek above timberline, VII-28-70 (R. Taylor, JS); Hayden Pass, 10,700', VII-22-71 (J. Scott); Hunts Lake, VIII-5-70 (R. Taylor, JS); West Creek Lake, 12,000', VIII-11-70 (J. Scott). *Gilpin Co.:* S. of Tolland, VII-11-58, 1♂ (D. Eff, LACM); W. of Kingston, VIII-19-51, 2♂ (D. Eff, LACM); James Peak, VII-26-52, 1♂ 1♀ (AMNH). *Grand Co.:* Skyline Drive, near Kremmling, VII-6-69, 2♂ (D. Eff, LACM); Roger's Pass, VIII-17-62, 1♀ (D. Eff, LACM). *Gunnison Co.:* Cottonwood Pass, 12,000', VII-19-64 (S. Ellis); Cumberland Pass, 12,025', VII-17-62, 4♂ 2♀ (J. Shepard); Emerald Lake, VIII-8-61 (J. Scott); Monarch Pass, VIII-6-61, VII-29-67 (J. Scott). *Gunnison-Chaffee Co.* line: ridge summit, near radar towers, just E. of Monarch Pass, VIII-14-70, 10♂ (S. Ellis & O. Shields). *Hinsdale Co.:* E. Rio Grande Pyramid, VII-28-71 (J. Scott); Stony Pass, 15 mi. NW of Rio Grande Pyramid, 12,000', VII-20-68 (S. Ellis). *Larimer Co.:* Trail Ridge Rd., 12,300', VIII-24-71 (J. Scott). *Park Co.:* Buffalo Peaks, VIII-12-73 (J. Scott). *Pitkin Co.:* Independence Pass, VII-15-59, 1♂ (N. La Due). *Pueblo Co.:* Greenhorn Peak, ca. 12,000', VII-13-70 (J. Scott).

WYOMING. *Carbon Co.:* Medicine Bow Peak, Snowy Range, 11,500', VII-17-62, 2♂ 1♀ (J. K. Windsor, LACM).

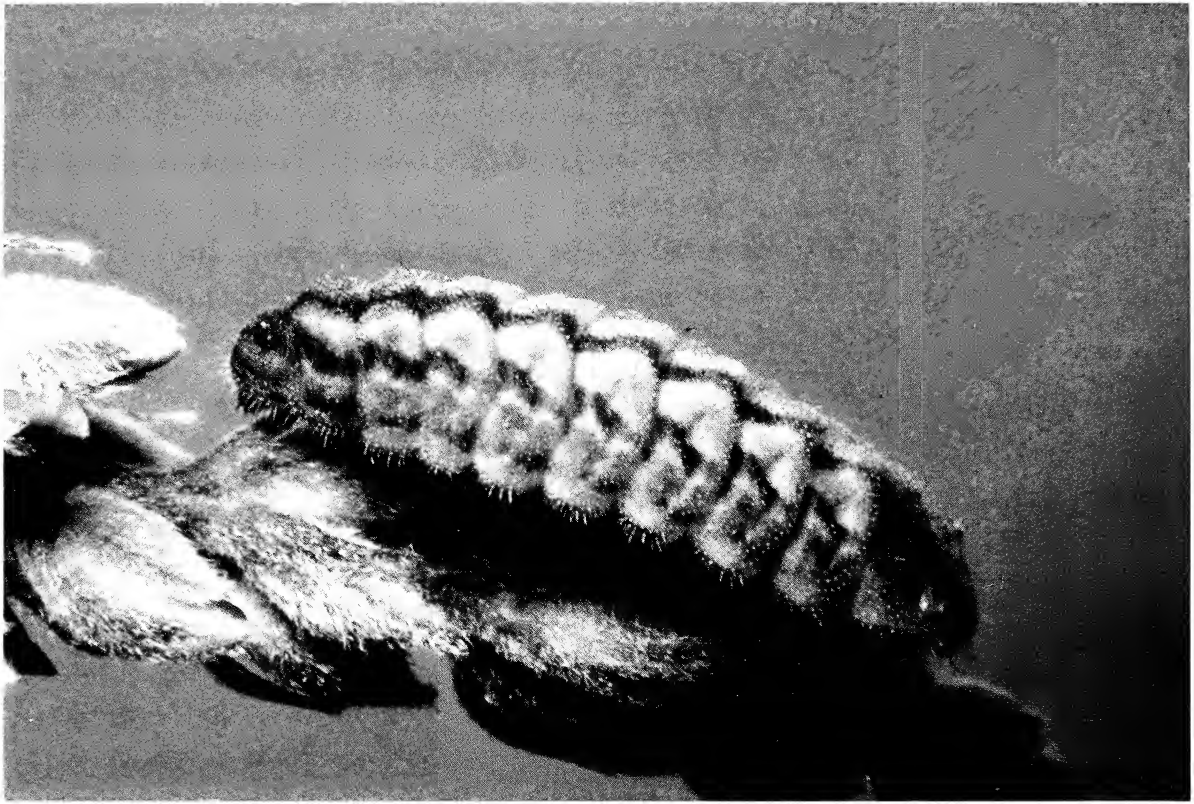

Fig. 1. Last instar larva of *P. shasta*. Photo by E. S. Ross.

Table I

Foodplants of *P. shasta.* Key to observation abbreviations: O = female oviposited on plant, or ova found on plant; L = larvae found on plant; P = pre-oviposition behavior by female toward plant noted.

SUBSPECIES	FOODPLANT	LOCALITY	OBSERVATION
shasta	*Astragalus purshii* Dougl.	Ebbetts Pass, Alpine Co., Calif.	O, L
	Astragalus whitneyi Gray	Donner Pass, Placer Co., Calif.	O, L
	Lupinus arbustus Dougl. (see text)	Donner Pass, Placer Co., Calif.	L
	Lupinus breweri Gray var. *bryoides* C.P. Sm. in Jeps.	Bodie Hill, Mono Co., Calif.	P
	Lupinus lyallii Gray	Tioga Pass, Mono-Tuolumne Cos., Calif.	O
minnehaha & Great Basin populations	*Astragalus calycosus* Torr.	Toquima Range, Nye Co., Nevada	O
	Astragalus calycosus Torr. var. *mancus* (Rydb.) Barneby	East Humboldt Range, Elko Co., Nevada	O
	Astragalus kentrophyta Gray var. *elatus* Wats.	Wasatch Plateau, Sanpete Co., Utah	P
	Astragalus kentrophyta Gray var. *implexus* (Canby) Barneby	White Mts., Inyo-Mono Cos., Calif.	O, P
	Astragalus newberryi Torr.	Santa Rosa Range, Humboldt Co., Nevada	P
	Astragalus platytropis Gray	Toiyabe Range, Lander Co., Nevada	O
	Astragalus purshii Dougl.	Warner Mts., Modoc Co., Calif	P
	Oxytropis parryi A. Gray	Snake Range, White Pine Co., Nevada	O
	Trifolium gymnocarpum Nutt.	Snake Range, White Pine Co., Nevada	O
	Trifolium monoense Greene	White Mts., Inyo-Mono Cos., Calif.	O
pitkinensis	*Trifolium dasyphyllum* T. & G.	Baldy Peak and Hermit Pass, Custer Co., Colorado	O

INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbrevations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

Illustrations: Color must be submitted as a transparency (i.e., slide) ONLY, the quality of which is critical. On request, the editor will supply separate detailed instructions for making the most suitable photographic ilustrations. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors **must** plan on illustrations for reduction to the 4 x 6½" page. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink at least twice the final size. Include a metric scale or calculate and state the actual magnification of each illustration as printed. Each figure should be cited and explained as such. The term "plate" should not be used. Each illustration should be identified as to author and title on the back, and should indicate whether the illustration be returned.

Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

Review: All papers will be read by the editor(s) & submitted for formal review to two references. Authors are welcome to suggest reviewers, and if received submit name & comments of reviewers.

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Volume 17 *Number 2* *Summer, 1978(80)*

IN THIS ISSUE

COVER ILLUSTRATION: Satellite photograph of the San Luis Valley, John F. Emmel and Oakley Shields.

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Journal of Research on the Lepidoptera *17(3):141, 1978(80)*

Editorial

We hope you are pleased with our new format, turned out on our own typesetting and layout equipment. Although there were substantial blunders in 17 (2), we have since reorganized and feel assured such will be minimal henceforth. Lorraine Rothman is now managing editor on a full time professional basis and is responsible directly for typesetting, correcting galleys, layout, page proof, and interface with our printer. She will also set up the news, notices and announcement section, which will be printed as an informal supplement. Please address all pertinent material to the attention of Mrs. Rothman at the editorial office.

The double mailing including this issue concludes Vol. 17 (1978). We have sufficient material for Vol. 18 (1979) which is forthcoming within the next two to three months. We do, however, require manuscripts for Vols. 19 (1980) and 29 (1981). We see no impediment to being on schedule in 1981 excepting appropriate papers, which we now solicit. We anticipate an average of eight color plates per volume, which will be text plates. Color covers have been discontinued. We do solicit any graphic material you have which is suitable for a cover.

Our referee system is in operation, every paper being submitted to two referees. Although many papers in Vol. 17 were not refereed, most in 18 have been. Those not reviewed by the peer system after 17(3) will be so indicated. Further, for all critical papers and reviews, rebuttal will be provided. We welcome comments and constructive criticism, and will publish relevant letters concerned with such matters in order to maintain an enlightened audience.

Although the thrust of this journal is non-taxonomic, we receive a share of strict taxonomic manuscripts. In the course of the review process, and from our independent observation of several publications, there is a substantial area of disparate practice on the matter of format and style. Since science is an endeavor depending on clear transmission of information, it would seem most efficient to adopt a uniform format and style, at least where formal description itself is involved. We have worked up a tentative instruction sheet and sample which we intend to adopt for conformity, clarity, and efficiency. We intend the instructions to be all inclusive. These are in process of review by concerned referees for comment. We will make them available to any concerned reader for comment, and will, prior to Vol. 20, implement the acceptable version. It will be clear that we take no issue with **content**, only **format**.

Journal of Research on the Lepidoptera 17(3):142-144, 1978(80)

Observations on the Apparent Lek Behavior in Costa Rican Rainforest *Perrhybris pyrrha* Cramer (*Pieridae*).

Philip J. DeVries

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Abstract.—Large numbers of male *Perrhybris pyrrha* (Pieridae) butterflies briefly chase other species having the same tiger-striped color pattern as *P. pyrrha* females; showing that visual cues are important as a primary recognition system for those male butterflies when seeking a mate. The presence of abundant host-plant and adult food resources in a concentrated area could initiate a lek.

Introduction

A lek is a communal display or display area where males congregate for the purpose of attracting and courting females and to which females come to mate (Wilson 1975). Leks have been reported in mammals, fish, frogs, (Emlen and Oring 1977), birds (Lack 1968), and some insects (Dodson 1975, Campanella and Wolf 1974, Lloyd 1966). However they have not been described for any species of butterfly. Here I describe apparent lekking behavior in the males of the neptropical butterfly, *Perrhybris pyrrha* Cramer.

Observations

Observations on *Perrhybris pyrrha* were made at La Sirena, in the lowland rainforest of Parque Nacional Corcovado, (Osa Peninsula, Costa Rica), from 3 to 18 July and 1 to 6 August 1977. *P. pyrrha* is common on the Pacific side of Costa Rica and occurs in the forest from sea level to about 800 meters elevation. Females of *P. pyrrha* share the same basic tiger-striped color pattern and lazy flight behavior as many heliconiine and ithomiine butterflies (presumably being part of a mimetic complex), whereas males appear white in flight and act like more ordinary new world Pieridae such as *Phoebis*, *Ascia*, *Appias*, and *Leptophobia*.

Each morning at about 7 a.m., one and one half hours after sunrise, more than 100 *P. pyrrha* males were observed flying around a large vine-covered tree about 35 meters tall at the forest edge on the north side of the airstrip. Each male would fly from the crown of the tree to approximately 3 meters above the ground and then return to the top of the tree. None settled on the vegetation; all remained continuously in flight making the assemblage very conspicuous as far away as 100 meters. At the same time of day, about 10 meters away from the tree, a small patch of *Lantana camara* L. (Verbenaceae) flowers was being visited by *Heliconius ismenius* Latr. (Heliconidae), *Mechanitis isthmia* Bates (Ithomiidae), *Anartia fatima* Fab. (Nymphalidae) as well as *P. pyrrha* females. From one to five males would leave the "display" tree and chase butterflies having the tiger-striped color pattern when they flew near the display. When *P. pyrrha* males chased *H. ismenius* or *M. isthmia*, the chase was short in duration (five to thirty seconds) and the males would return to the display. There were two types of chases of *P. pyrrha* females: On the one hand males chased the female for a short distance and then returned to the display, on the other the males chased the female out of sight, either into the forest or above the forest canopy. I did not observe the end of any of the long chases.

This activity of displaying and chasing continued until about 10 a.m., at which time both male and female *P. pyrrha* dispersed into the forest behind the display tree. This forest has a dense understory of *Capparis isthmensis* Eichl (Capparidaceae) trees, the host-plant of *P. pyrrha* (DeVries unpublished). In previous intermittant field observations during the course of one year, this has been the only habitat in Parque Corcovado where I have seen *P. pyrrha*. This possibly represents a restriction of the adults to the vicinity of the host-plant. Other forest habitats only 300 meters away have no *P. pyrrha* in them and the host-plant is rare in these forests. While in the forest butterflies do not form similar aggregations to my knowledge, nor have I seen them court. Rather, they are dispersed throughout the understory.

I observed these displays almost daily during the first half of July. On several days in early August, M. L. Higgins noted them as well. In November 1977 there was no evidence of display behavior, although eggs, larvae, and adults of *P. pyrrha* were abundant.

Discussion

I suspect that the two classes of chased *P. pyrrha* represented mated and virgin females, respectively. The length of time the males pursue females can be used as a measure of female receptivity in *Heliconius* (L. E. Gilbert, personal communication and my own observations), and in other butterfly genera (Scott 1974). Assuming the long chases end with mating and chases (short or long) are courtship displays, then the group display of *P. pyrrha* males described here would, in a broad sense, satisfy the definition of a lek. No spatial organization was discernable within the volumne of the display. Those males in the display closest to the ground at the time a female flew toward the *L. camara* patch could be in a better position to chase and court than those males that were at the top of the tree owing to the greater distance needed for the latter to travel to a passing female. Since differential mating success is the most important parameter in lek biology, further study is needed to determine if this exists among males of *P. pyrrha* at the display. The high host-plant density and the nearby nectar source could be initiators to the development of lek behavior in *P. pyrrha* when coupled to a large population of adults. Interestingly, the sex ratio of *P. pyrrha* appears to be predominatly female in field reared material (personal observation) and in greenhouse cultures as well (Craig Jordan, University of Texas). The fact that the *L. camara* patch was no longer in heavy flower in November 1977 could it itself explain the absence of the display at that time.

Acknowledgments: This manuscript benefited greatly from comments and discussion by D. H. Janzen, F. G. Stiles, H. Clench, and L. D. Gomez. I thank R. Sanford, M. L. Higgins, and G. Vega Arias for field assistance. I dedicate this paper to Arthur Blake who never got a chance to see the Osa. This study was supported by NSF grant DEB 77-04889.

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Male Genitalic illustrations and notes on the Larentiinae (Geometridae) of Missouri[1]

Roger L. Heitzman and Wilbur R. Enns[2]

Dept. of Entomology, Univ. Mo.-Columbia 65211

Abstract.—Male genitalic illustrations of 28 species are presented. Eleven of these have never been illustrated before. Another 9 replace inadequate or partial illustrations. The remaining 8 show individual or geographic variation. The male genitalia of 4 species and the female genitalia of 17 species are described for the first time. New state species distribution records and new synonymies are also presented. Species treated and recorded as captured in Missouri total 36 in number.

This is one of several articles (Heitzman and Enns, 1977, 1978) based on a review of the Missouri Larentiinae. These should be consulted for information on state distributions, flight periods, larval plants, new nomenclature combinations, keys, adult illustrations and explanatory figures.

The taxonomic importance of the genitalia has stood the test of time as one of the best means of separating species of Lepidoptera. Many groups would still be hopelessly confused if it were not for the presence of diagnostic genitalic characters which have so often led to the discovery of other, more subtle, characters. In the Larentiinae, the large genera *Hydriomena* and *Eupithecia* are 2 excellent examples. Genitalia are useful for distinguishing species and genera but often not much help at subfamily or family levels. Their potential for grouping higher categories has often been investigated. Many similar-looking genital structures have envolved again and again independently, and this can be very deceptive. It is the instability of these characters that has made them so very useful for distinguishing closely related species. There are those who will contend that the external genitalic structure is but a pleiotropic by-product of the genes, but the genitalic similarities and stability of structure usually run parallel to other characters examined between close taxa in the Geometridae. There appears to be a great deal of inconsistency in the artifical grouping of the Larentiinae,

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[1] Contribution from the Missouri Agricultural Experiment Station, Entomology Research Museum, Journal Series No. 8084. Approved by the Director. Received for publication.

[2] Graduate Research Assistant and Professor, respectively.

particularly on the generic level, even when other characters are taken into account. This is probably true for most groups of Lepidoptera.

The genitalic terminology employed here basically follows that of Pierce (1914). Unless otherwise stated, genitalic descriptions are based on Missouri specimens. All illustrations are of Missouri specimens.

The illustrations are intended to be accurate representations, and were made with the aid of a microprojector (WILD M5-Zeichentubus®). The genitalic drawings show the ventral view, except for the aedeagus which is usually shown in its dextral aspect. All drawings were made by the senior author.

Xanthorhoe lacustrata (Guenee) (Fig. 1)

Forbes (1948, Fig. 156) illustrated the value of the male genitalia of *lacustrata.* It is without accompanying data, and shows minor variation in comparison to Missouri specimens. Both the valvula and costa are shaped differently.

Female with ostium wide; operculum scobinate; bursa copulatrix globular, with oblong signum; neck of bursa long.

Earophila multiferata (Walker) (Fig. 2)

Euphyia multiferata, Heitzman, 1973.

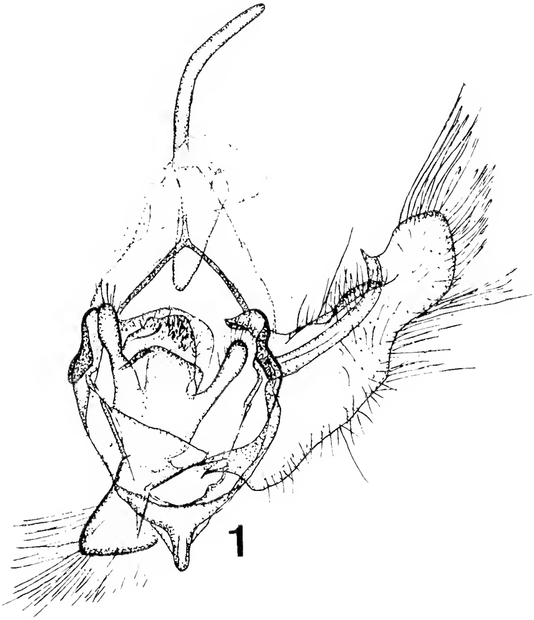
Apparently, the male genitalia of this species have not been illustrated before. A comparison of the species with *vasiliata* (Guenee), *switzeraria* (Wright), and *pectinata* (Rindge) in Rindge's 1967 revision reveals numerous differences. In *multiferata* the valve is stouter, the juxta is basally bilobed, cristae are present, the transtilla lobes are larger, and the costa does not end in a free spine.

Female with ostium wide, funnel-shaped, sclerotized on venter; ductus bursae short, with a sclerotized collar open on venter; ductus seminalis small, arising at base of collar; bursa copulatrix large, membranous irregular, with several lobes; signum an irregular, heavily sclerotized plate on left side near middle.

Euphyia centrostrigaria (Wollaston) (Fig. 3)

Apparently, the male genitalia of this species have not been illustrated before. The clasping unit is unusual in that the valves arise so low and the uncus has a dorsally directed curvature.

Female with ostium very wide, funnel-shaped, sclerotized; ductus bursae heavily sclerotized, rather wide, long; bursa copulatrix membranous, globular.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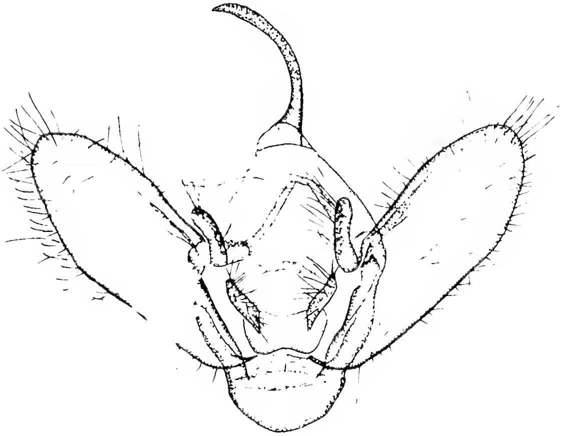
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Fig. 1 — *Xanthorhoe lacustrata* (Guenee)
Fig. 2— *Earophila multiferata* (Walker)

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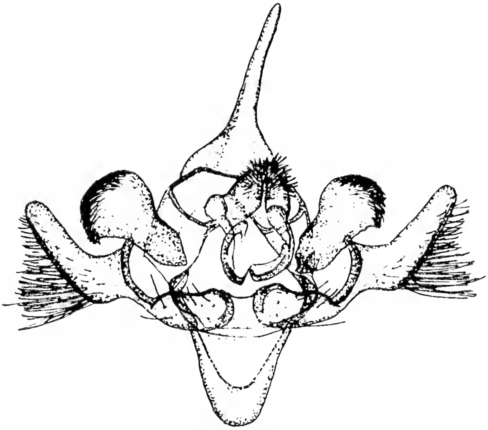

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Fig. 3 — *Euphyia centrostrigata* (Wollaston)

Fig. 4 — *Orthonama obstipata* (Fabricius)

Orthonama obstipata (Fab.) (Fig. 4)

Nycterosea obstipata, Heitzman, 1973.

The male genitalia were illustrated before by Pierce (1914, Pl. 47). Unfortunately, no data are associated with this figure. The discrepancies between his illustration and ours are almost incredible. There is a great need to look at a lot of material from all over the world to see how many species are really involved. Considering the worldwide distribution of this species, it could possibly be explained away as a phenomenon of inter-population variation. However, we strongly suspect that two or more species are involved, unless his illustration is inaccurate or based on a mutation. The genitalia are highly modified leaving the homologies uncertain.

Camptolina stellata (Guenee)

Apparently, the male genitalia of this species have not been illustrated or completely described. The following description of the male genitalia is based on Louisiana specimens:

Uncus short, bilobed, with sparse setae; anal tube strong, with a pair of mildly sclerotized rods; anellus lobes long, with many setae at tips; juxta bifid, with setae; saccus extended, triangular; valve narrow at base, expanded at apex; sacculus enlarged, heavily sclerotized, with a short, cephalad projection at base, a long, narrow process distally; valvula membranous, with setae thick on upper half; costa normal; aedeagus long, extremely narrow, with 2 long, weak cornuti and a scobinate tip.

Female with ostium wide, funnel-shaped; ductus bursae extremely long, narrow, sclerotized; bursa copulatrix a large, membranous sack with a stellate signum possessing 7 large spines.

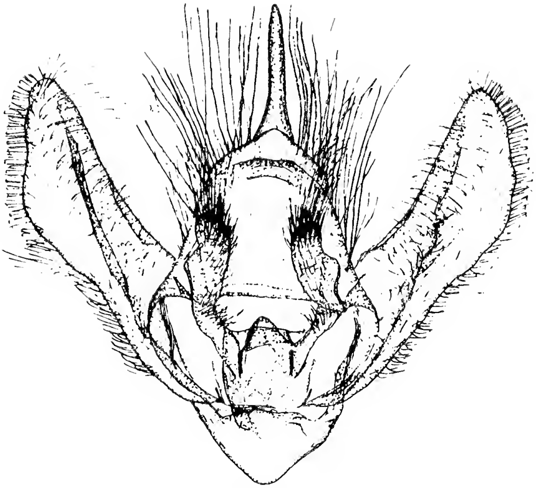
Venusia comptaria Walker (Fig. 6)

Apparently, the male genitalia of this species have not been illustrated before. The genitalia appear nearly identical to *Hydrelia inornata* (Hulst) except that the annellus lobes are lacking.

Female with ostium small, sclerotized; ductus bursae very long, narrow, heavily sclerotized, bursa copulatrix ovular to globular, membranous, with an elongate signum near neck on venter, rest of bursa with very fine spines.

Hydrelia inornata (Hulst)

The male genitalia are almost identical with *Venusia comptaria* Walker except for the presence of long, narrow annellus lobes that curl



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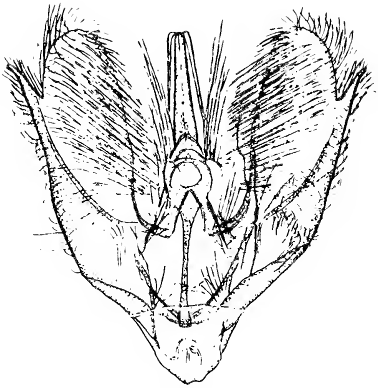

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Fig. 5 — *Trichodezia albovittata* Warren
Fig. 6 — *Venusia comptaria* Walker

laterad and have short setae mesally. The aedeagi of both species are long and narrow without cornuti.

Female with ostium wide, funnel-shaped, sclerotized laterally; ductus bursae fairly long, heavily sclerotized, but with a membranous ring in middle; bursa copulatrix large, membranous, with a stellate signum on venter near middle and a small patch of spines on dorsum near neck.

This species was previously recorded as far west and south as Kentucky. It has been taken recently in several eastern Missouri counties.

Hydrelia albifera (Walker)

Female with ostium wide, funnel-shaped; ductus bursae very long, lightly sclerotized, with a distal collar; bursa copulatrix oval, bulging to left, with a large, ovate patch of spines on distal right and wide bar of spines on proximal left.

This species was previously recorded as far south as Pennsylvania. A single fresh female specimen was recently taken in west central Missouri. The *Hydrelia albifera* of the 1973 checklist referred to a *Metasiopsis* sp.

Trichodezia albovittata Warren (Fig. 5)

Apparently, the male genitalia of this species have not been illustrated before. The aedeagus is large with numerous cornuti.

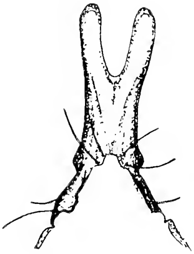
Female with ostium wide, sclerotized; ductus bursae short, membranous; bursa copulatrix huge, elongate, sclerotized, covered with minute spines; signum an arrowhead-shaped plate on venter near middle, pointing distally, resting on proximal end.

Hydriomena bistriolata Zeller (Fig. 9)

McDunnough (1954) has already adequately described and illustrated the genitalia of both sexes of the Nearctic *Hydriomena* species. Our illustrations show only minor variation in uncal shapes and setal arrangements, which probably fall within the bounds of individual variation.

Hydriomena mississippiensis McDunnough (Fig. 8)

There is little evidence for the specific status given this taxon. McDunnough (1952) did not acknowledge the affinities of *mississippiensis* to *bistriolata* Zeller, and presented no satisfactory differences. The minor differences in the uncus do not correspond to any unique external characters. The bursa of the female holotype of *bistriolata* is twisted and distorted.



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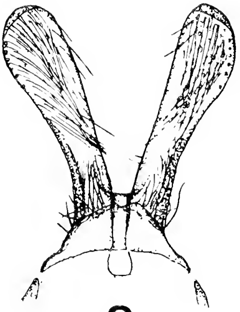

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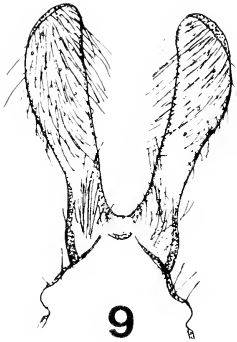

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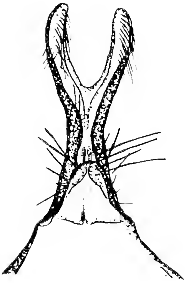

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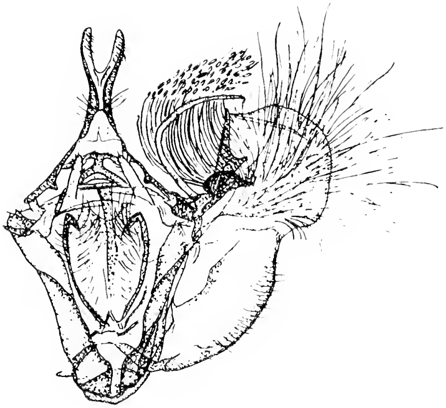

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Fig. 7 — *Hydriomena pluviata meridianata* McDunnough

Fig. 8 — *H. mississippiensis* McDunnough

Fig. 9 — *H. bistriolata* Zeller

Fig. 10, 11 — *H. transfigurata manitoba* Barnes and McDunnough

Hydriomena pluviata meridianata McDunnough (Fig. 7)

All Missouri specimens examined posses the lateral protuberances at the base of the uncus and the uncal forks are always naked.

Hydriomena transfigurata manitoba Barnes & McDunnough (Figs. 10, 11)

Hydriomena transfigurata, Heitzman, 1973.

This subspecies always has setae on the venter of the uncal forks. McDunnough (1954, Fig. 50) apparently omited this character.

Hydria prunivorata (Ferguson) (Fig. 12)

The male genitalia of this species were previously illustrated by Ferguson (1955, Fig. 1) from New York. Our illustration varies to some degree in most characters, the form of the juxta varying the most.

Coryphista meadi (Packard) (Fig. 13)

Apparently, the male genitalia of this species have not been illustrated before. The genitalia are very similar to those of *Hydria prunivorata* (Ferguson).

Female with ostium small, funnel-shaped; ductus bursae long, with some variable spining; bursa copulatrix a small, membranous sack with an oval signum.

Rheumaptera hastata (L.) (Fig. 14)

The male genitalia of this species were previously illustrated by McGuffin (1973, Fig. 57a-d). Our illustration varies to some degree in most characters, the form of the juxta and the length of the sacculus process varying the most.

Ecliptopera atricolorata (Grote & Robinson) (Fig. 16)

Diactinia atricolorata, Heitzman, 1973.

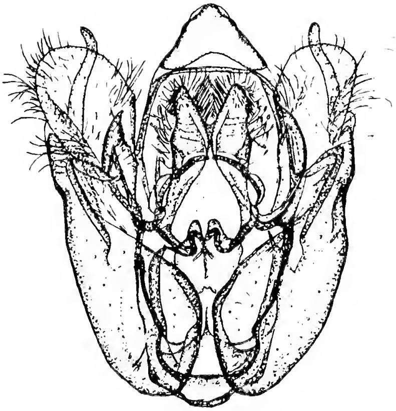
Apparently, the male genitalia of this species have not been illustrated before. The aedeagus is stout, with a band of small cornuti.

Female with ostium weak; ductus bursae short, membranous; bursa copulatrix large, oblong, with an irregular, scotinate signum.

Archirhoe neomexicana (Hulst)

Apparently, the male genitalia of this species have not been described before. The following description of the male genitalia is based on the examination of Arizona specimens:

Uncus long, narrow, apex expanded, with many short setae; anal tube wih broad sclerotization; transtilla expanded medially; manica heavily



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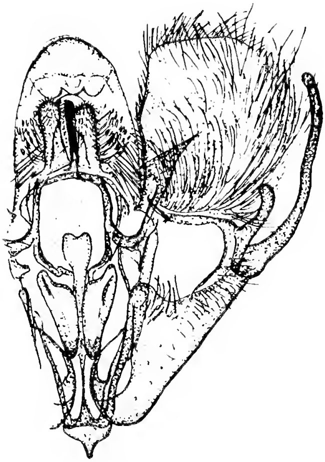

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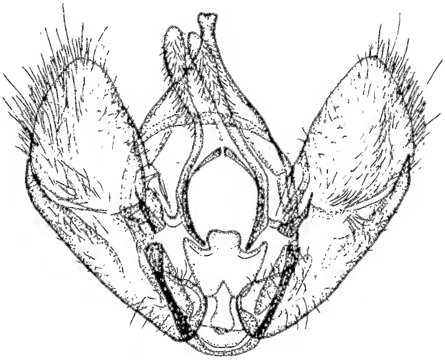
Fig. 12 — *Hydria prunivorata* (Ferguson)
Fig. 13 — *Coryphista meadi* (Packard)



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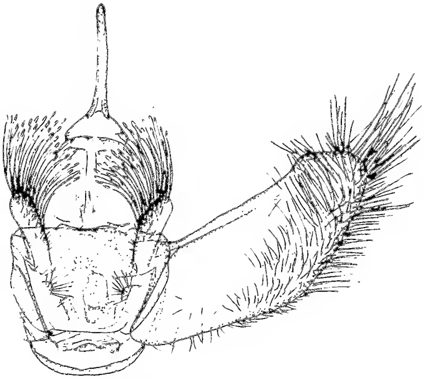

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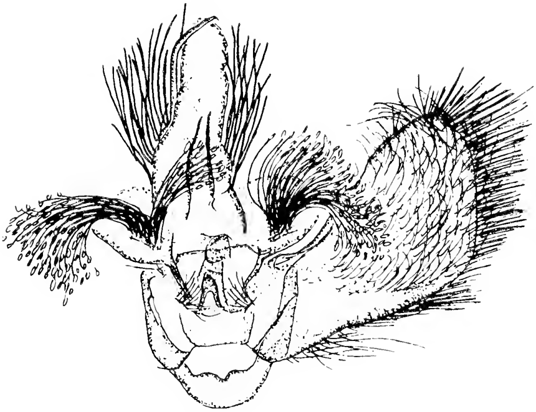
Fig. 14 — *Rheumaptera hastata* (Linnaeus)
Fig. 15 — *Eulithis diversilineata* (Hubner)



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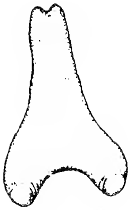

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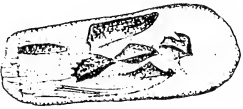

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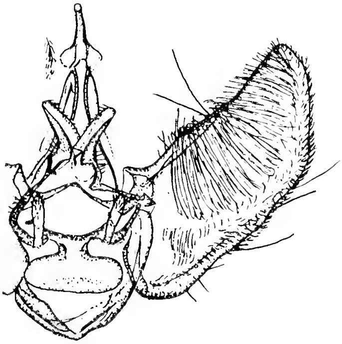

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Fig. 16 — *Ecliptopera atricolorata* (Grote and Robinson)
Fig. 17-19 — *Eupithecia geminata* Packard

spined; anellus lobes short, tipped with long setae; juxta plate V-shaped posteriorly, with lateral arms anteriorly; saccus small, thick, tapering to a point; sacculus enlarged, heavily sclerotized, curling over base of central framework; valvula reduced, membranous, with many long setae, particularly on outer edge; costa thick, heavily sclerotized, with a long, pointed process, thickened at its middle; aedeagus long, curved; opening large, rugose, vesica with about 6 cornuti on 1 side, and 2 larger ones on other side; coremata very large.

Female with ostium funnel-shaped, rugose, membranous, with sclerotized, lateral pieces; ductus bursae with long, sclerotized collar open on venter; bursa copulatrix large, membranous, without signum.

This southern species has not previously been recorded from Missouri.

Eulithis diversilineata (Hubner) (Fig. 15)

Lygris diversilineata, Heitzman, 1973.

Apparently, the male genitalia of this species have not been illustrated before. The aedeagus is simple, without cornuti. The only consistent difference we can find in the genitalia between this species and *E. gracilineata* (Guenee) is the more lightly sclerotized genitalia of *diversilineata.*

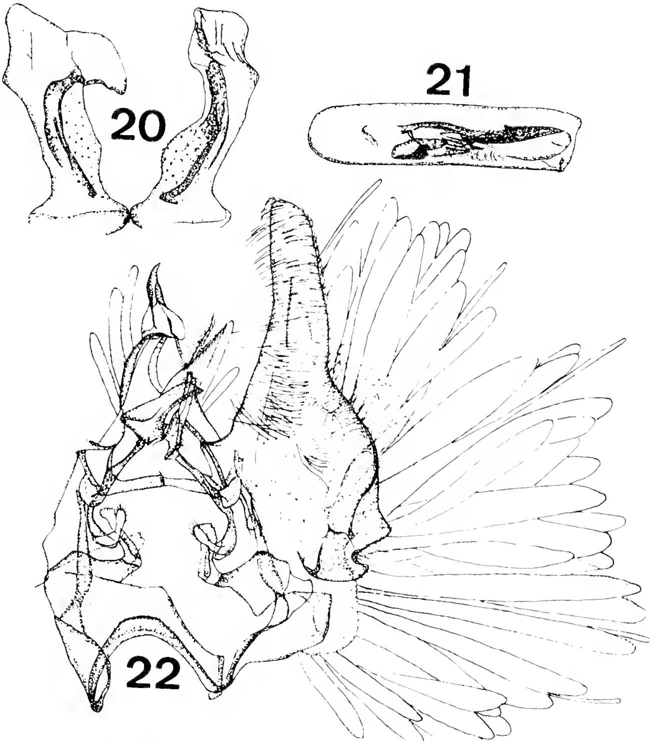
Female apophyses weak; ostium weak; ductus bursae rather short, with a long sclerotized collar open on dorsum; bursa copulatrix large, peanut-shaped; signum a thin, finely spinose line on proximal half of right side; ductus seminalis small, arising on neck just above signum on right side.

Eulithis gracilineata (Guenee)
Lygris gracilineata, Heitzman, 1973.

The genitalia of this species vary from *diversilineata* (Hubner) only in being more heavily sclerotized. There is no solid evidence favoring the validity of these two taxa being treated as species.

Eupithecia miserulata Grote (Figs. 20-22)

The genitalia of most of the Nearctic species of this genus have been previously illustrated by McDunnough (1949); however, of the clasping unit he only outlined the valve. We have noted that the species also vary in the formation of the saccus and the labidal pads and papillae. The shape of the valve varies considerably within a given species and is not generally a reliable character. There appears to be some individual variation in nearly all characters.



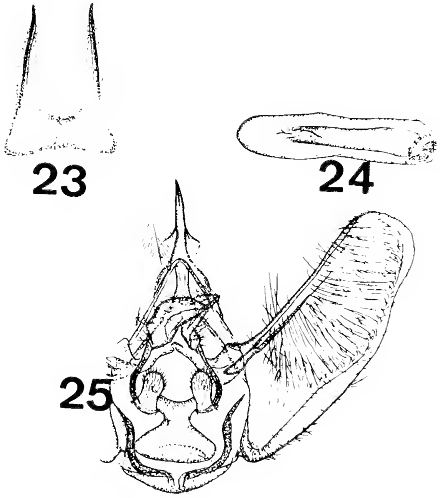
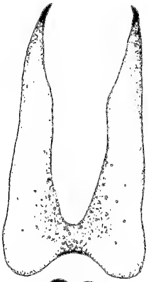


Fig. 20-22 — *E. miserulata Grote*
Fig. 23-25 — E. rindgei McDunnough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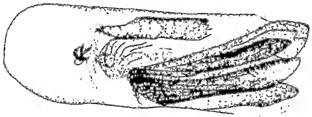
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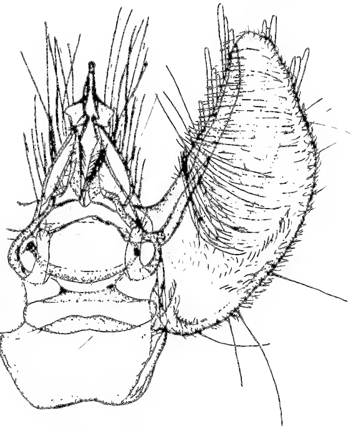
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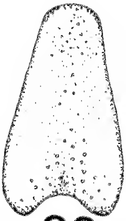
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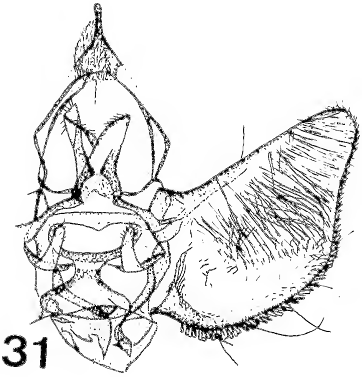
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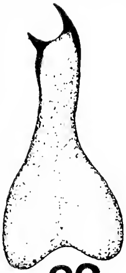
Fig. 26-28 — *E. herefordaria* Cassino and Swett
Fig. 29-31 — *E. swetti* Grossbeck



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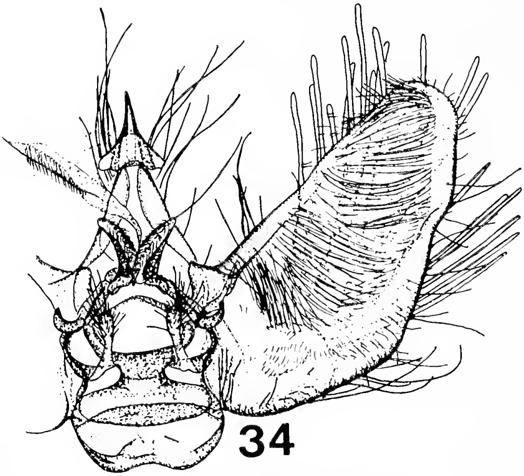

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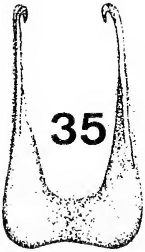

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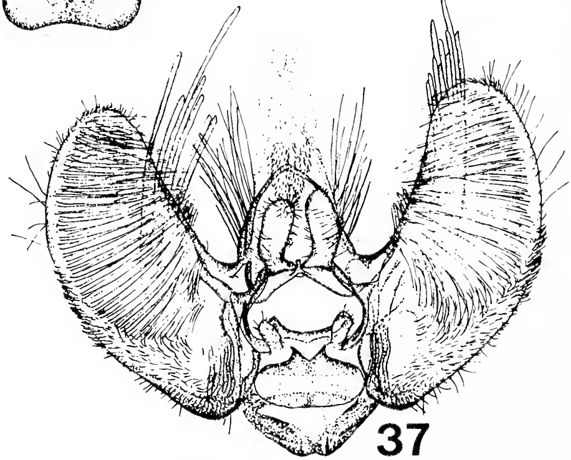

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Fig. 32-34—*E. fletcherata* Taylor
Fig. 35-37—*E. coloradensis* (Hulst)

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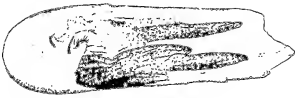

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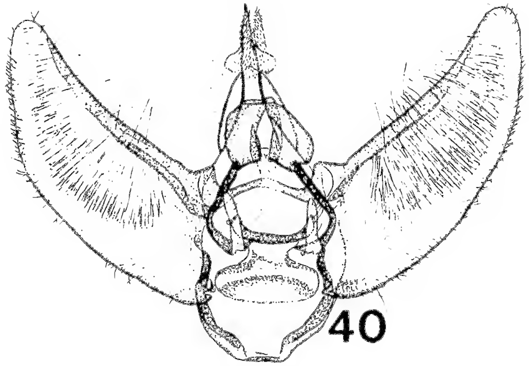

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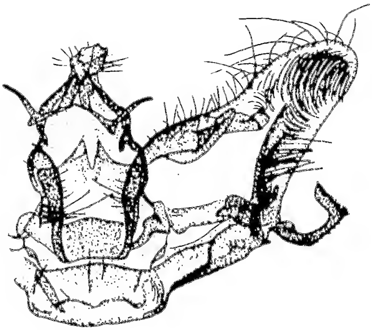

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Fig. 38-40—*E. jejunata* McDunnough
Fig. 41—*Horisme intestinata* (Guenee)

In *miserulata,* McDunnough's illustration (loc cit., Fig. 4A) of the eighth sternite lacks the deeply sclerotized pieces found in the rods.

Eupithecia jejunata McDunnough (Figs. 38-40)

The eighth sternite and aedeagus were illustrated by Rindge (1956, Figs. 1, 2). The clasping unit has not been illustrated before.

This species has previously been recorded from only 4 southern states. Lewis Co., Missouri (northeast section) now becomes the northernmost point of its range.

Eupithecia fletcherata Taylor (Figs. 32-34)

The eighth sternite illustrated by McDunnough (1949, Fig. 5E) differs somewhat in shape and lacks the heavy sclerotization of the claws.

Western Missouri is a considerable extension in the previously recorded range of *fletcherata.* It was last recorded only so far southwest as Pennsylvania.

Eupithecia peckorum Heitzman & Enns

Eupithecia palpata, Heitzman, 1973.

The genitalia of this species were illustrated in the original description (1977, Figs. 1-3, 7).

Since the original description, a fall specimen was discovered that had been taken from Jasper Co., Mo.

Eupithecia coloradensis (Hulst) (Figs. 35-37)

Eupithecia strattonata, Heitzman, 1973.

The eighth sternite illustrated by McDunnough (1949, Fig. 4E) differs somewhat from ours in shape and does not show the hooked apices.

Eupithecia herefordaria Cassino & Swett (Figs. 26-28)

The eighth sternite illustrated by McDunnough (1949, Fig. 7E) does not compare well with those we observed; however, other characters suggest this is the correct placement.

Eupithecia swetti Grossbeck (Figs. 29-31)

The eighth sternite of McDunnough's figure (1949, Fig. 9E) shows some variability in the shape.

Eupithecia geminata Packard (Figs. 17-19)

The eighth sternite of McDunnough's figure (1949, Fig. 9F) differs slightly in shape and lacks the basal pits.

This species has been recorded over much of the Nearctic region, but never before in Missouri.

Eupithecia rindigei McDunnough (Figs. 23-25)

Eupithecia dichroma-johnstoni complex, Heitzman, 1973.

The clasper and aedeagus do not compare well with McDunnough's illustration (1949, Fig. 14H). The valve of the holotype is much longer, narrow, and more curved than in our observations. Also, the aedeagus appears longer, with a differently formed vesica.

This species was previously known only from California. It has now been taken as far east as central Missouri. These widely disjunct populations appear very similar when looking at the female genitalia and external characters. The primary is about 2 mm smaller in the western population. There is some doubt as to the correct taxonomic treatment of the Missouri population.

Eupithecia cocoata Pearsall

Eupithecia indistincta, Heitzman, 1973.

The male genitalia of this species were just recently illustrated (Heitzman and Enns, 1977). The female genitalia were illustrated by McDunnough (1949, Fig. 14I).

Horisme intestinata (Guenee) (Fig. 41)

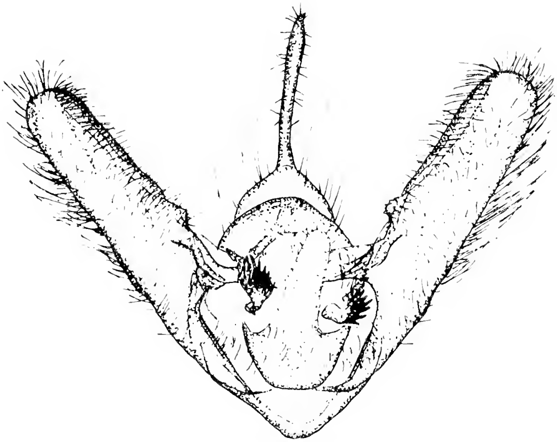
Apparently, the male genitalia of this species have not been illustrated before. Pierce (1914, Pl. 35) illustrated 4 European species of *Horisme.* They are close to each other, but show only vague relationships with *intestinata.*

Female with ostium wide, funnel-shaped, without striations; ductus bursae very long, becoming much wider than ostium, possessing a variable, dorsal lineof spines; bursa copulatrix a rather small sac, ⅓ size of the ductus bursae, embedded with many large spines.

Heterophleps triguttaria Herrich-Schaffer (Fig. 42)

Apparently, the male genitalia of this species have not been illustrated before. It is very close to *H. refusata* (Walker) but lacks the gnathos.

Female with ostium wide, membranous; ductus bursae short, with a terminal collar; neck of bursa copulatrix long, heavily sclerotized, with 6 longitudinal ridges; bursa sack oval-shaped, membranous; ductus seminalis arising from membranous tip of bursal neck.



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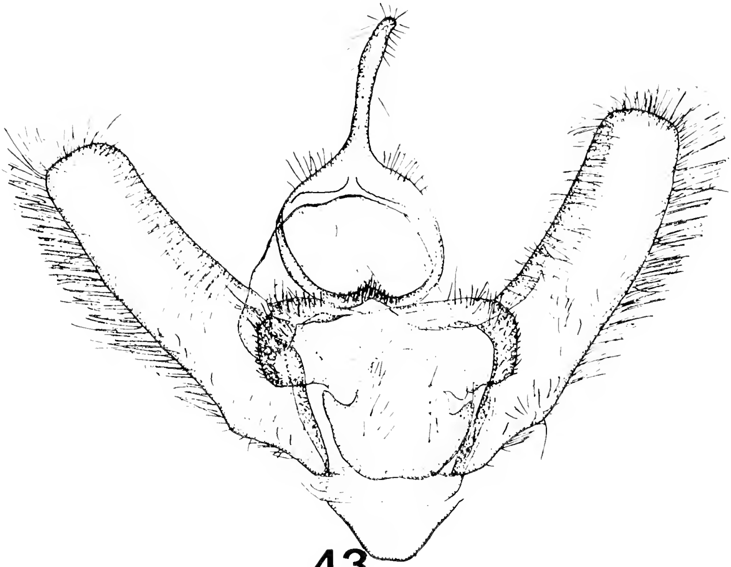

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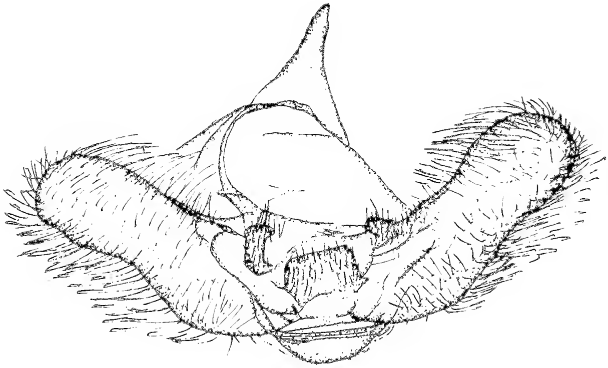
Fig. 42—*Heterophleps triguttaria* Herrich-Schaffer
Fig. 43—*Heterophleps refusata* (Walker)



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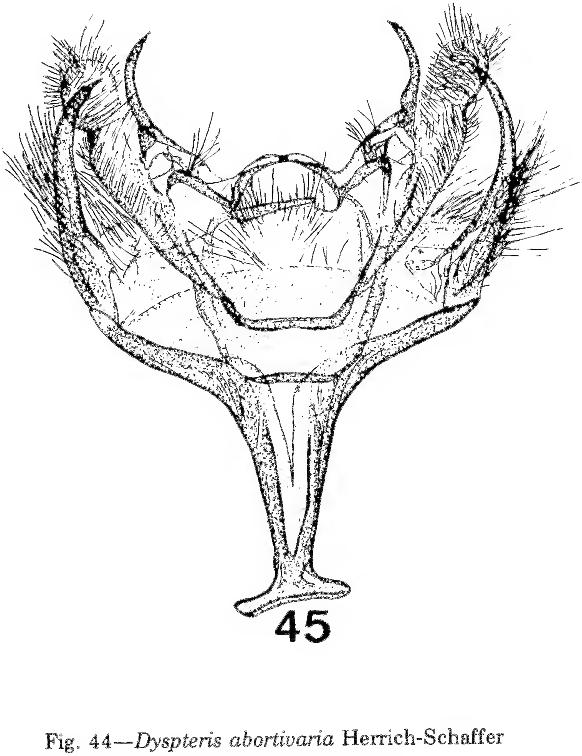

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Fig. 44—*Dyspteris abortivaria* Herrich-Schaffer
Fig. 45—*Eubaphe mendica* (Walker)

Heterophelps refusata (Walker) (Fig. 43)

Apparently, the male genitalia of this species have not been illustrated before. There appear to be good generic similarities.

Female with ostium wide, sclerotized on venter; ductus bursae short, membranous; bursa copulatrix very elongate, membranous, with a ring of 11 short, longitudinal ridges at proximal third, 9 of these protruding centrally with a flat, upcurving spine, 2 on left and 1 on venter without spines; ductus seminalis arising near ostium on right side.

Dyspteris abortivaria Herrich-Schaffer (Fig. 44)

Apparently, the male genitalia of this species have not been illustrated before. The genitalia are very simple and weakly sclerotized.

Female with ostium small, lightly sclerotized ventrally; ductus bursae short, membranous; bursa copulatrix oval, membranous.

Eubaphe mendica (Walker) (Fig. 45)

The genitalia have been previously illustrated by Fletcher (1954, Figs. 3, 18, 23, 51). Our illustration varies in nearly all respects, but there is considerable individual variation.

Eubaphe unicolor (Robinson)

The genitalia have been illustrated by Fletcher (1954, Figs. 17, 21, 48).No male specimens have yet been taken in Missouri.

Acknowledgements: The following institutions and individuals are extended sincere thanks for their support and for providing specimens for examination: Dr. Douglas C. Ferguson, Systematic Entomology Laboratory, USDA, Washington, D.C.; Dr. W. C. McGuffin and Mr. Klaus Bolte, Biosystematics Research Institute, Ottawa, Ontario, Canada; Dr. D. S. Fletcher,British Museum (Natural History), London, England; Mr. James Houser, Clayton Museum of Science and Natural History, Clayton, Missouri; Mr. Joseph E. Francka, Missouri State Department of Agriculture, Jefferson City; Dr. C. V. Covell, Jr., University of Kentucky, Louisville; Dr. William Peck, Central Missouri State University, Warrensburg; Dr. J. H. Shaddy, Northeast Missouri State University, Kirksville; Dr. R. A. Hart, Northwest Missouri State University, Maryville; Dr. Richard Borchelt, Southeast Missouri State University, Cape Girardeau; Mr. J. Richard Heitzman, Independence, Missouri; Mr. Rae Letsinger, Sarcoxie, Missouri; Dr. Stephen Dykstra, Overland Park, Kansas; Dr. Michael Dykstra, Canton, Missouri; Dr. Richard Fellows, Louisville, Kentucky; Mr. Edward Riley, Dr. Siegfried Thewke, Mr. Michael Carroll, Dr. James Huggans, Dr. Wilfred Craig, and all others associated with the University of Missouri-Columbia who assisted in this undertaking.

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Journal of Research on the Lepidoptera *17(3):168-169, 1978(80)*

Observations on *Phoebis Sennae* (Pieridae)

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In San Diego County *Phoebis sennae marcellina* (Cramer) is not a common butterfly (Emmel & Emmel, 1973, Butterflies of Southern California, Natural History Museum of Los Angeles County). In occasional years a fair number may fly through in late summer or fall and become temporarily established. They generally die out during the winter, and *P. sennae* becomes extremely scarce again for several years.

In mid-September 1976 a large storm, hurricane Kathleen, struck the coast of Baja California and deposited several inches of rain throughout Baja and southern California. By the first of October *P. sennae* had become quite common in the extreme southwestern corner of San Diego County. From 6 to 20 were seen daily, flying due North at a rapid pace, seldom stopping to visit flowers. They continued to pass by for about three weeks, gradually becoming less abundant. Five specimens were captured during this time: four males (Sept. 30, Oct. 1, 10, 23) and one female (Oct. 1). Three of the specimens were quite worn. Since *P. sennae* is known to migrate in the tropics (Klots, 1951, Field Guide to the Butterflies, Houghton Miffin Co., Boston), I assume that these adults were migrating. I was quite surprised to find that the undersides of the male specimens were very plain, almost the same as in the eastern subspecies *eubule*. The female was albinic, as were several other females I observed. Also, Fred Thorne, a resident of El Cajon, reported observing albinic females ovipositing on *Cassia* sp. in his yard in mid-October. However, none of the typical yellow-orange *marcellina* females were observed.

During the second week of November, *P. sennae* was once again abundant. From 15 to 35 individuals were seen daily for about the next two months. The number dwindled gradually. Most of these, but not all, were flying northward. Many of them visited the Red Cape Honeysuckle *(Tecomaria capensis)* near my home. The following were captured with no difficulty:

Date	Males	Females
Nov. 8	3	2
Nov. 10	1	3
Nov. 18	1	
Nov. 29		1
Dec. 1	1	
Dec. 10	1	1
Dec. 28		1
Jan. 17	1	

Since there had been no more of the southern storms which occasionally "blow" odd material into this area, and since many of these specimens were quite fresh, this brood was probably progeny of the *P. sennae* that came through in late September and October. Fred Thorne's observations of ovipositing females also strengthen this assumption.

The undersides of this locally produced brood were very heavily marked as in typical *P. sennae marcellina* that is occasionally taken in this area. None of the females were albinic. The first *P. sennae* to fly through must have been *marcellina* to judge from their apparent offspring, and not *eubule* as they appeared to be.

P. sennae marcellina is generally characterized as the western subspecies with much heavier markings on the ventral surface of the wings. However, I found this to be true only with the locally produced brood.

By the end of February *P. sennae* had disappeared. All spring and summer I waited for another locally produced brood that never materialized.

During a collecting trip to southern Arizona in early August of 1977 I collected many *P. sennae.* All the females were albinic and all the males had the very plain ventral surface. From these few observations it appears that *P. sennae marcellina* in the southwestern United States has two seasonal forms: (1) plain ventral surfaced males and albinic females flying in summer and fall, and (2) typical heavily marked males and typical yellow-orange females in a late fall or winter brood.

Journal of Research on the Lepidoptera *17(3):170-171, 1978(80)*

A Study of the Meiotic Chromosomes of *Ixias Marianne* (Cramer) (Pieridae)

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Abstract.—The haploid Chromosome number of *Ixias marianne* was determined as 28 which forms the first report in this genus from India. The mean of the terminalization coefficient and chiasma frequency are .912 and .989 respectively.

The genus *Ixias* is represented by three species in the Indian region: *marianne, pyrene* and *verna* (Talbot 1939). Although the chromosome numbers of some Indian members of the family Pieridae, to which *Ixias marianne* (Cramer) belongs, were reported by Gupta (1964) and Rishi (1973), none of the three Indian representatives of the genus *Ixias* were studied by them. Hence, this paper aims at reporting the chromosome number and certain details of meiosis of *Ixias marianne* (Cramer) which has not been reported heretofor in the genus *Ixias* from India.

All the material used for the present study was collected from the fields and hills around Perecherla, near Guntur town. Testes of adults were dissected in cold Ringer's solution and squashed in 2% aceticorcein without prefixation. The preparations were made semipermanent by sealing the coverglasses to the slides.

Counts on well-spread metaphase I plates clearly show 28 bivalents (fig. 1). Most are dumb-bell shaped with almost terminalised chiasma. However, cross bivalents with single interstitial chiasma and ring bivalents with two terminal chiasmata were also noted in some preparations.

Maeki and Ae (1966) reported the haploid chromosome number of *Ixias pyrene familiaris* Butler from the Himalayan region as 28 of which seven bivalents are distinctly smaller than the remainder. Though the chromosome number of *I. marianne* agrees with the above related species, no such size distinction was observed among bivalents.

In spite of large number, smaller size and almost spherical shape of the chromosomes, an attempt has been made to record certain features of meiosis. Of 5656 bivalents observed in 202 nuclei from 10 specimens; 210 were cross bivalents, 132 ring bivalents and 213 separated into distinct univalents. The terminalization coefficients ranged fom .876 to .953 with a mean of .912 and the chiasma frequency ranged from .964 to 1.029 with a mean of .989. By the time spermatocytes reach late diakinesis and early metaphase most of the bivalents assume the usual dumb-bell shape with a terminal chiasma.

The haploid chromosome number 28 of *Ixias marianne* deviates from 31 which is the modal number for both th family Pieridae and the order Lepidoptera.

I wish to acknowledge and thank Dr. A. S. Murthy for supervision, the authorities of Nagarjuna University for providing facilities, and the University Grants Commission (New Delhi) for financial support. I further wish to dedicate this paper to the memory of my father Shri N. Narayana Raju, who passed away Dec. 1, 1977.

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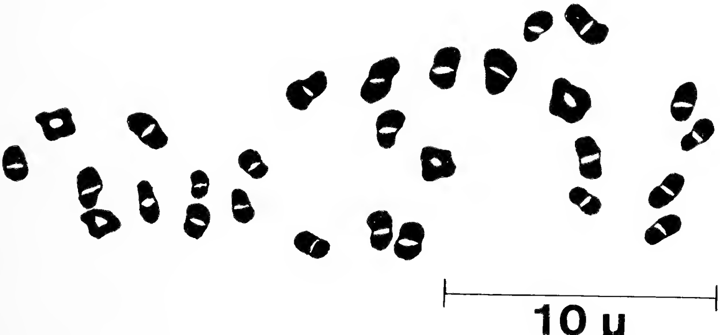

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Fig. 1 — Metaphase I stage of *Ixias marianne* (Cramer).

Journal of Research on the Lepidoptera 17(3):173-179, 1978(80)

The Larva of *Acronicta spinigera* Guenee (Noctuidae)[1]

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Abstract.—The mature larva of *Acronicta spinigera Gn. (Lepidoptera: Noctuidae) is described. Ulmus american* L. was found to be an acceptable food plant. Ova eclosed in 7 days and the larva reached maturity in 23 days.

Acronicta spinigera Gn. is uncommon in collections and prior to this paper nothing was known of the life history. The species occurs from Canada and Maine to Wisconsin and south to Texas (Forbes, 1954). Smith & Dyar, 1898, and Forbes, 1954, placed *A. spinigera* next to *A. pruni* Harris. Smith & Dyar considered *A. pruni* to be the "nearest ally" to *A. spinigera*. McDunnough, 1938, placed *A. spinigera* next to *A. morula* G. & R. The discovery of the larva corroborates this position.

A. morula larvae (Fig. 2) have dorsal protuberances on the first, fourth, and eighth abdominal segments, whereas *A. spinigera* (Fig. 1) larvae have them on the first and eighth segment, those on the third and fourth segment being only weakly developed. Furthermore, both types of larvae have the vertex of the head reddish-orange in color.

A female of *A. spinigera* was taken at ultra-violet light on 27 June 1977 in the Adirondacks, 6 miles east of Indian Lake, 1820 ft., Hamilton County, New York. Two days later, 12 flattened ova were laid. The larvae eclosed in seven days and were offered *Populus tremuloides* Michx. and *Malus* sp. The first instar larvae initially fed on *Malus*, but did poorly on it and many died. *Populus tremuloides* was rejected and finally *Ulmus americana* L. was offered. The sole remaining larva fed readily on the elm and attained full size in 23 days.

The illustrations that accompany the descriptions of the last larval instar were drawn to scale using the grid system. All scale lines represent 0.5 mm. The terminology and abbreviations follow Godfrey (1972).

General (Fig. 1). Head 4.62 mm wide. Total length 38 mm (fully distended, preserved larva). Abdominal prolegs present on third through sixth segments. Integument clothed with minute, short spines on dorsal two-thirds. Body protuberant dorsally on abdominal segments one and eight, slightly so on four and five. Spiracle A-8 0.36 mm high.

Coloration (living material). General head and body color light gray. Vertex of head reddish orange. Abdomen with a pale orange, broken middorsal line, setal insertions white, spiracles black.

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Fig. 1. *Acronicta spinigera*, Adirondack Mts., New York: photograph of living, ultimate instar larva.

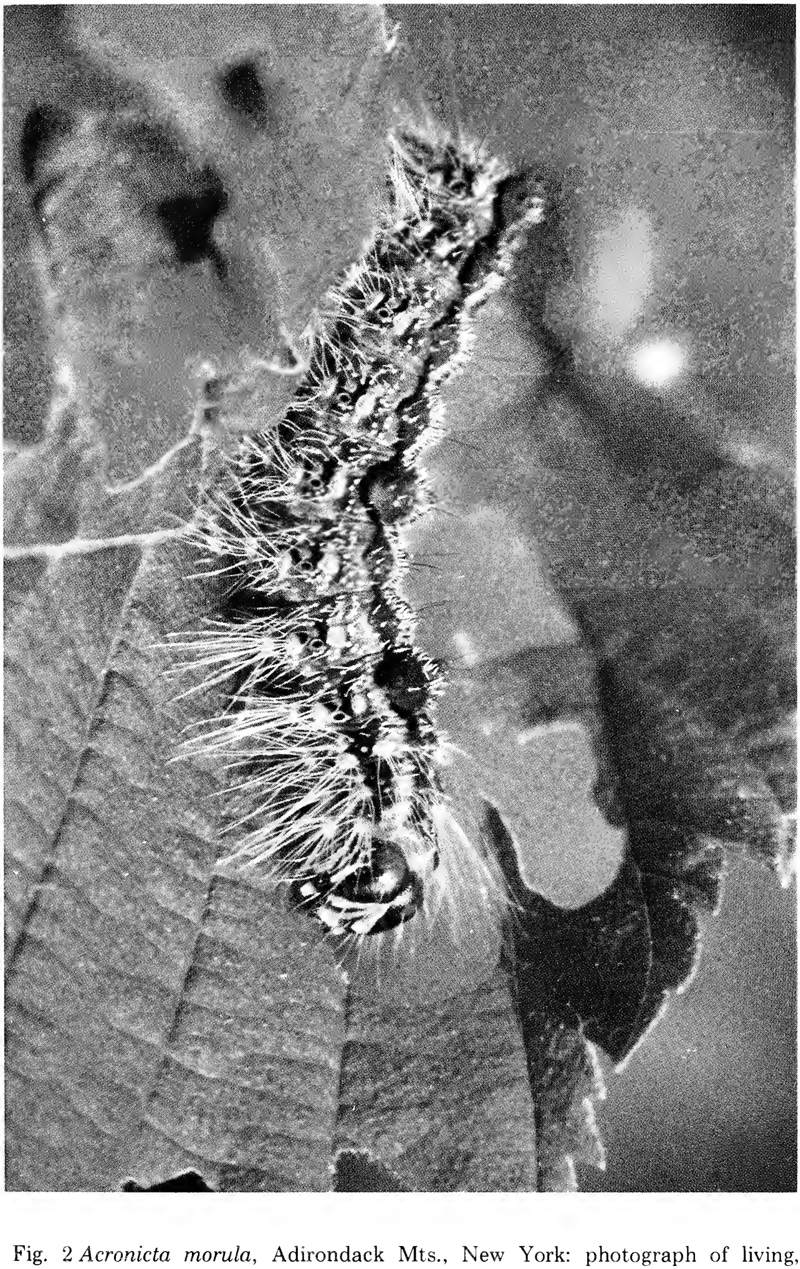


Fig. 2 *Acronicta morula*, Adirondack Mts., New York: photograph of living, ultimate instar larva.

Head (Fig. 3). Epicranial suture 1.83 times height of frons. Second adfrontal seta (Af-2) posterior to apex of frons. Pigmented areas present near apex of frons and between seta F1 and margin of frons. Vertex reddish orange. Upper two-thirds of head capsule with scattered black markings. Ocellar interspaces between Oc1 & Oc2 and Oc2 & Oc3 subequal; Oc3 to Oc4 equal to diameter of Oc3; Oc4 to Oc6 approximately 3x diameter of Oc4; Oc4 to Oc5 approximately 4x diameter of Oc4.

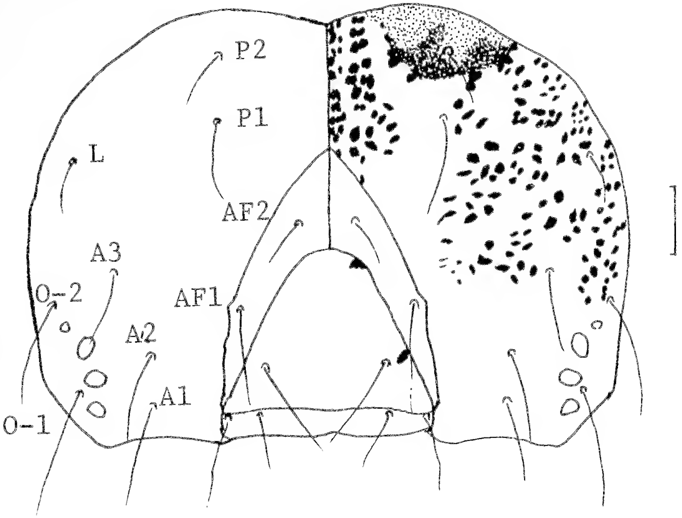
Mouthparts. Hypopharyngeal complex (Fig. 5): spinneret with distal lip surpassing second segment of labial palpus, bare; stipular setae (S) subequal in length to Lps, twice length of seta Lp-1, and equal to seta Lp-2. Distal region of hypopharynx covered with fine spines; proximomedial region without spines; proximolateral region bearing a single row of about 17 spines. Mandible (Fig. 4): with a second ridge parallel to the first and with a deep concavity proximad to second ridge. Several shallow concavities present between first (marginal) and second ridge of teeth and again between second ridge and concavity.

Thoracic segments. Segment T-1 (Fig. 6): numerous secondary setae present, those on shield with insertion on pale pinacula. Prespiracular and remaining setae with insertion on lightly pigmented verrucae. Shield with a dark pigmented posterior margin and a lightly, pigmented anterior margin; with separate isolated patch near posterior margin in middle. Shield, verrucae, and dorsal two-thirds of segment with numerous, minute spines. T2 & T3 with dorsal verrucae with setal insertions in pale patches. Subdorsal and lateral veruccae with setal insertions not differentiated from ground color. Tarsal claws cleft at mid point forming a flat ledge.

Abdominal segments. Ab-1 (Fig. 7): with dorsal protuberance composed of verrucae corresponding to D1 & D2 on both sides of body. Verrucae D1 & D2 heavily pigmented with setal insertions on pale, circular areas. Verruca D1 with 3 setae, D2 with 6 setae, Sd-1 with 5 setae, L-1 with 6 setae and L-2 with 4 or 5 setae. Numerous scattered setae present, especially below spiracular line. Segments three and four slightly protuberant dorsally, eight markedly protuberant. Crochets uniordinal, 23-25 per third abdominal proleg, 23-25 per fourth, 29 per fifth, and 14-15 per sixth.

Material examined: One specimen, 6 miles east of Indian Lake, 1820 ft., lat. 43°45′30″ long. 74°10′14″, Hamilton Co., New York, 26 June 1977, from ovum of female collected, determined and reared by T. L. McCabe.

3



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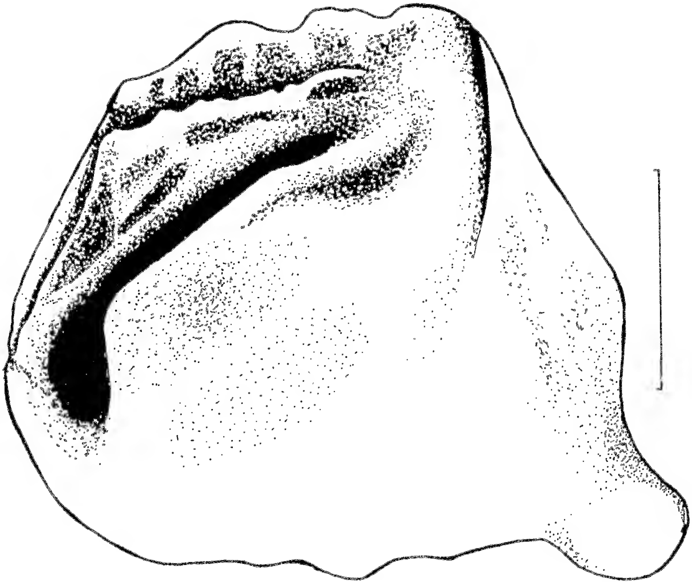
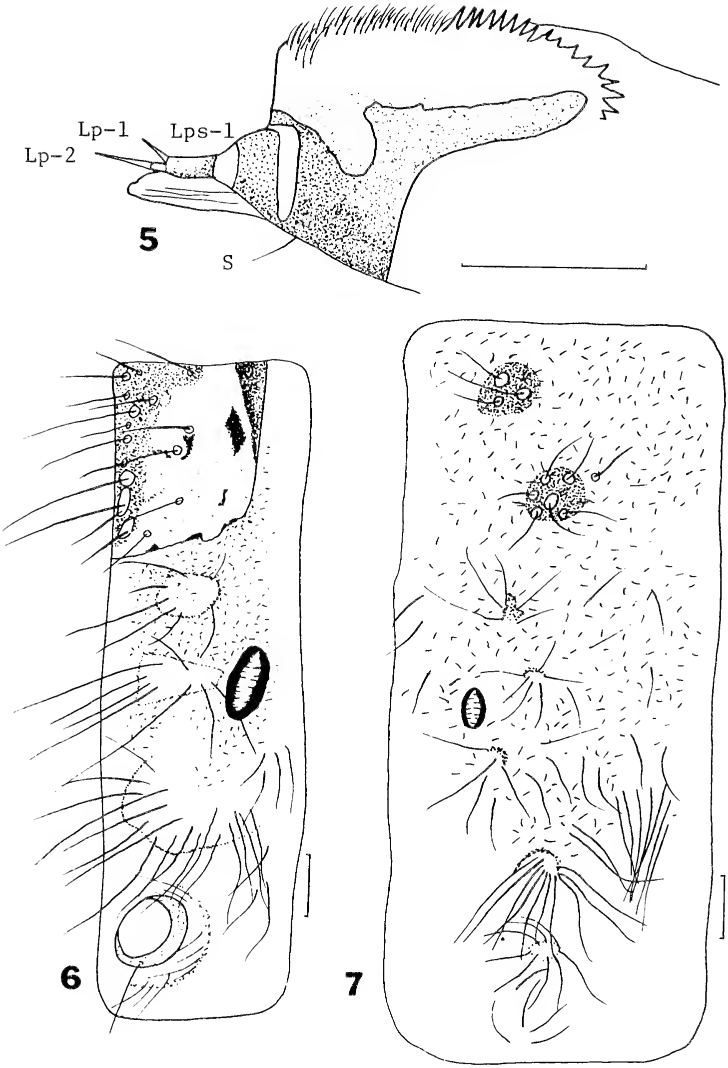


Figs. 3-4. *Acronicta spinigera*, Adirondack Mts., New York: 3. frontal aspect of head; 4. oral aspect of left mandible.



Figs. 5-7. *Acronicta spinigera*, Adirondack Mts., New York: 5. left aspect of hypopharyngealcomplex; 6. left setal arrangement of prothorax; 7. left setal arrangement of first abdominal segment.

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Digestive enzymes of a sugarcane borer, *Chilotraea infuscatellus* Snell.

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Abstract.—The enzymes maltase, sucrase, trehalase, beta-fructosidase, chymotrypsin, aminotripeptidase, leucine aminopeptidase, prolinase, glycyl-L-leucine dipeptidase and flycyl-glycine dipeptidase were detected in the salivary glands of *C. infuscatellus.* The gut showed activity for all these in addition to beta-glucosidase, alpha-galactosidase, beta-galactosidase and trypsin. The significance of synthesis of oligosaccharides in the gut is to avoid hyperglycaemia. Out of the four distinct substrate specific alpha-glucosidases, three-(maltase, sucrase and trehalase) were present; raffinose was not hydrolysed by sucrase. Separate enzymes were involved for the hydrolysis of sucrose, raffinose and melibiose; alpha-galactosidase did not hydrolyze raffinose.

Introduction

Although a wide variety of digestive enzymes have been reported in the Class Insecta, a detailed knowledge of the presence of peptidases in this group is still not available. The present paper gives a detailed account of the digestive enzymes found in the salivary glands, and in the contents and tissues of the three different regions of the gut of the last larval instar of *Chilotraea infuscatellus.* It also attempts to clarify the ambiguity regarding glycosidase specificity.

Materials and methods

The larvae of *C. infuscatellus* were collected from infested sugarcanes in the vicinity of Lucknow and reared at 27°C on sliced sugarcane which were changed daily. Enzyme extracts were prepared and enzymes assayed as described previously (Agarwal, 1975 & 1976).

Results

The results are summarised in Table I, which gives qualitative and comparative quantitative data of various enzymes. In the salivary gland sucrase, trehalase, beta-fructosidase, chymotrypsin, aminotripeptidase, leucine aminopeptidase, prolinase, glycyl-L-leucine dipeptidase and glycyl-glycine dipeptidase, and a very weak activity of maltase were detected.

Many workers have noted the formation of oligosaccharides in the gut of insects and their presence in the excreta. Duspiva (1953), Srivastava and Auclair (1962), Yang and Davis (1968), and Ishaaya and Swirski (1970) are of opinion that oligosaccharides are produced by the action of invertase on sucrose. It has been further demonstrated that oligosaccharides can also be synthesized in presence of melezitose, melibiose (Srivastave, 1966), and maltose (Takanona and Hori, 1974). Gilmour (1961) and Dadd (1970) regarded that the synthesis of oligosaccharides is due to transglycolysation reaction of alpha-glucosidases. On this basis Gilmour (1961) regarded invertase as a sugar-transferring enzyme and also thus recognized two types of (functionally different) (Dadd, 1970) alpha-glucosidases in insects. In *C. infuscatellus* the synthesis of oligosaccharide is due to reverse catalysis by some glycosidase's when glucose alone or glucose and fructose both are produced or present in high concentrations in the gut, as has been pointed out in *Sesamia inferens* (Agarwal, 1976). Further the chromatograms of Srivastava and Auclair (1962) further support these observations although their conclusions were different.

The synthesis of oligosaccharides in an insect seems to be an important measure in limiting the diffusion of monosaccharides in the gut when present in excess and are not required by the insect. Thus the insect is able to avoid hyperglycaemia and ultimately excretes the oligosaccharide to avoid its hydrolysis again. Such a feedback mechanism enables the insect to feed on a variety of diets having different percentages of digestable carbohydrates. The sugarcane borer larva can feed on sugarcane throughout the year, during which period the percentage of sucrose varies widely in its sugarcane foodplant.

Gilmour (1961) did not include trehalase among the digestive enzymes of insects. Bursell (1970) has pointed out that in insects trehalase is capable of catalysing the synthesis of trehalose, but this pathway is probably not of physiological significance. Trehalose is found in a high concentration in the haemolymph of insects, but is generally absent in their normal food. Thus some of its may diffuse into their gut (Wyatt, 1967), but when there is a shortage of carbohydrates in the diet the loss may affect their survival. Thus trehalase in the gut of insects may be a necessity to avoid such loss, because as soon as trehalose would diffuse from the haemolymph in the gut, it would be broken into glucose which would be resorbed (by diffusion gradiant) as glucose is practcally absent in the haemolymph. Trehalase thus functions as a digestive enzyme.

C. infuscatellus has three distinct substrate specific alpha-glucosidase (maltase, sucrase and trehalase), observations which support my previous report (Agarwal, 1976) where it has been clearly demonstrated that in insects instead of a generalized alpha-glucosidase there are at least four distinct substrate specific alpha-glucosidases.

Weidenhagen's (1932) conservative view regarding the specificity of glycosidases has been supported by various workers. Fraenkel (1940), Krishna and Saxena (1962), Khan and Ford (1962 and 1967), Banks (1963) and Evans and Payne (1964) are of opinion that alpha-galactosidase which hydrolyzes melibiose may hydrolyze raffinose also and that beta-fructosidase which hydrolyzes raffinose may also hydrolyze sucrose. Dadd (1970), and Takanona and Hori (1974) doubted the hydrolysis of sucrose by beta-fructosidase, but recognized the concept of the hydrolysis of raffinose by alpha-galactosidase. The confusion regarding the specificity of alpha-galactosidase and beta-fructosidase continued probably because distinct situations were not detected in any insect. In *C. infuscatellus* (Table II) the midgut tissue hydrolyzed melibiose and sucrose and did not hydrolyze raffinose, this means that raffinose is not hydrolyzed either by sucrase or by alpha-galactosidase. The midgut contents hydrolyzed melibiose, sucrose and raffinose, an observation which establishes the presence of beta-fructosidase. Beta-fructosidase attacks raffinose between fructose and melibiose only, as is evident from the hydrolytic products of raffinose digestion by the salivary glands, foregut contents and hindgut contents.

Sugarcane contains a varity of free amino acids (Bhattacharya and Mukherjee, 1953) of which leucine, lysine and valine are regarded as essential. Three other essential amino acids (arginine, histidine and isoleucine) (Singh and Singh, 1964) are also provided by the hydrolysis of sugarcane proteins. Thus the larva gets only six essential amino acids from its diet. The remaining four essential amino acids (methionine, phenylalanine, threonine and tryptophan) (Wigglesworth, 1965; Dadd, 1970) may be regarded as non-essential or dispensable essential or if needed by the larva may be obtained by the transaminase system's generally present. In its haemolymph only phenylalanine was detected (Rakshpal and Singh, 1976) out of these four. This supports the suggestion that methionine, threonine and tryptohan may not be essential for the larva and it is capable of synthesizing phenylalanine.

In the foregut tissue only trehalase was detected, while the gut contents revealed all the enzymes of the salivary glands. The activity of matase, chymotrypsin and glycyl-L-leucine dipeptidase was very weak, however.

The midgut tissue showed activity of maltase, sucrase, trehalase, beta-glucosidase, alpha-galactosidase, beta-galactosidase, trypsin, chymotrypsin, aminotripeptidase and glycyl-glycine dipeptidase. Midgut contents showed a strong activity of all these in addition to beta-fructosidase, leucine aminopeptidase, prolinase and glycyl-L-leucine dipeptidase.

The hindgut tissue also gave evidence of the activity of sucrase, trehalase, chymotrypsin, aminotripeptidase and glycyl-L-leucine dipeptidase; while its contents showed the presence of all these enzymes along with beta-glucosidase, prolinase and glycyl-glycine dipeptidase; and a very weak activity of beta-galactosidase, beta-fructosidase, trypsin and leucine aminopeptidase.

When the sucrose contents were high in the diet of the larva, synthesis of a oligosaccharide took place in its gut which was excreted, but when the sucrose contents were low this synthesis was not observed. *In vitro* studies confirmed that the oligosaccharide synthesis took place when a high concentration of sucrose was taken as substrate.

When raffinose was hydrolyzed by the salivary glands, foregut contents and hindgut contents, melibiose and fructose were produced.

Discussion

C. infuscatellus feeds on sugarcane which contains a very high percentage of sucrose besides some glucose and fructose. Sucrose is therefore the most important many other carbohydrates, namely maltose, lactose, melibiose, trehalose and raffinose. For the hydrolysis of these metabolites, glycosidases are present in its gut. However, none of these carbohydrates are detected in sugarcane. Sucrase may therefore, be regarded as an obligatory enzyme while the other glycosidases are facultative.

The activity of sucrase is high throughout the gut of the larva, and its diet contains high percentage of sucrose. This relationship between sucrase and sucrose clearly supports the view of House (1965), Wigglesworth (1965) and Dadd (1970) that when in an insect there is high activity of any enzyme its substrate must be present in abundance in the diet.

At present little is known about the different aspects of proteases in insects. Now it can only be stated that in insects protein digestion takes place in three stages to librate amino acids, the raw materials essential for growth and maintenance of tissue proteins.

In *C. infuscatellus* some enzymes from the midgut did not reach the hindgut; suggesting that they are either denatured, digested, or self-hydrolyzed in the posterior part of the midgut. Similarly some enzymes of the hindgut contents were not detected either in hindgut tissue or in the excreta, which suggests denaturing, digestion or self-hydrolysis in the Posterior part of the hindgut. The Presence of some enymes in both hindgut tissue and contents, but their absence or low activity in the excreta, may be due to absorption in the hindgut (Agarwal, 1976). This would appear to be a conservative measure to retain as much enzyme protein as possible.

In the salivary glands of *C. infuscatellus* a large variety of enzymes were detected, all of which enter the foregut lumen along with the food. Thus the digestion of the food starts in the foregut as soon as the saliva is mixed with food-stuff. It has been claimed that the enzymes from the midgut can reach the foregut. In *C. infuscatellus* the enzymes from the midgut did not reach the foregut, since the enzymes exclusively of the midgut were not detected in the foregut. Further, antiperistalsis was never observed among the hundreds of larvae dissected. It is interesting to note that some enzymes are secreted only by the salivary glands and that they reach as far back as the hindgut via foregut and midgut.

From the proportionate hydrolysis in the three regions of the gut of the larva it is evident that the major part of digestion takes place in the midgut. The presence of a wide varity of enzymes in the gut normally not required may suggest its adaptive capacity, enabling survival under adverse nutritional conditions.

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TABLE I

Digestive enzymes in salivary glands and various gut regions of *Chilotraea infuscatellus*

Enzyme tested	Salivary glands	Foregut		Midgut		Hindgut	
		T	C	T	C	T	C
I. Carbohydrases							
1. Amylase (3.2.1.1)	–	–	–	–	–	–	–
2. Cellulase (3.2.1.4)	–	–	–	–	–	–	–
3. Alpha-glucosidases							
i. Maltase (3.2.1.20)		–		+	++	–	–
ii. Melezitase	–	–	–	–	–	–	–
iii. Sucrase (3.2.1.26)	+++	–	+	+++	+++	+	++
iv. Trehalase (3.2.1.28)	++	+	++	++	+++	+	++
4. Beta-glucosidase (3.2.1.21)	–	–	–	+	++	–	+
5. Alpha-galactosidase (3.2.1.22)	–	–	–	+	++	–	–
6. Beta-glactosidase (3.2.1.23)	–	–	–	+	++	–	
7. Beta-fructosidase (3.2.1.80)	++	–	+	–	+	–	
II. Proteases							
1. Aminopeptidases							
i. Leucine aminopeptidase (3.4.1.1)	++	–	+	–	+++	–	
ii. Aminotripeptidase (3.4.1.3)	++	–	+		+++	+	+
2. Carboxypeptidase (3.4.2.1)	–	–	–	–	–	–	–
3. Dipeptidases							
i. Glycyl-glycine dipeptidase (3.4.3.1)	+	–	+	+	++	–	+
ii. Glycyl-L-leucine dipeptidase (3.4.3.2)	++	–		–	++	+	+
iii. Prolinase (3.4.3.6)	+	–	+	–	++	–	+
iv. Prolidase (3.4.3.7)	–	–	–	–	–	–	–
4. Peptide peptidohydrolases							
i. Trypsin (3.4.4.4)	–	–	–	+	++	–	
ii. Chymotrypsin (3.4.4.5)	++	–		+	+	+	+

T – Tissue; C– Contents; –Activity absent; Very weak activity; + Weak activity; ++ Moderate activity and +++ High activity.

TABLE II
Hydrolysis of three glycosides in salivary glands and different gut regions of *Chilotraea infuscatellus*

Enzyme source	Glycoside hydrolyzed	Glycoside not hydrolyzed
Salivary glands	Raffinose and Sucrose.	Melibiose.
Foregut tissue	—	Melibiose, raffinose and sucrose
Foregut contents	Raffinose and sucrose.	Melibiose
Midgut tissue	Melibiose and sucrose.	Raffinose.
Midgut contents	Melibiose, raffinose and sucrose.	—
Hindgut tissue	Sucrose.	Melibiose and raffinose.
Hindgut contents	Raffinose and sucrose.	Melibiose.

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Ecological notes on the butterflies of the Churchill Region of Northern Manitoba

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Abstract.—The Churchill Region, substantially a tundra-taiga ecotonal community, consists of numerous geobotanical zones. This area's butterfly fauna includes at least 23 permanent breeding residents of various affinities, along with a number of casual, stray, or migrant species. Resident butterflies are discussed in terms of habitat zonation and distribution; observations are also made on aspects of the biology, ecology, and behavior of some of these species.

The butterfly fauna of the Churchill-Fort Churchill area is probably better known than that of any other subarctic location in north-central Canada. Masters (1971), in addition to reporting on his own activities during 1969 and 1970, presented data accumulated from other collections, published records and field notes, covering 15 separate seasons at Churchill. Included were the collecting expeditions of G. Shirley Brooks (1939-44 and 1946); Charles D. Bird, James Chilcott, and Alexander B. Klots (1951 and 1952); Frank H. and Paul Chermock (1961 and 1963); Vern Harper (1933); H. Elliot McClure (1936); and Cecil McCullough (1970). Ferris (1974) reported the occurrence of two previously uncollected species at Churchill. Collecting trips to the Churchill area have also been undertaken by A. E. Brower (1969) and C. S. Quelch (1968), among others. In addition, James Ebner maintained a collector in the area for several seasons during the mid-sixties.

In view of the amount of sampling done in the immediate vicinity of Churchill-Fort Churchill, it seems likely that few additions will be made to the area's faunal list. The biology, ecology, behavior, and zonal distributon of this area's butterflies have, however, received much less attention. Realizing that there is still much field work to be done in these areas, the present paper deals with habitat zonation in particular and notes certain observations relative to the biology, ecology, and behavior of some Churchill butterflies.

During the period 20 June to 20 July, 1974, the authors conducted ecological studies in this region. Many different collecting sites were visited, weather permitting. Not only were geographically separated locations sampled, but in attempt was made to note the species component of each particular plant community. Adult behavior and nectar sources were noted.

In addition to our observations, information from correspondence has been gained from A. E. Brower, John Ebner, Alexander B. Klots and C. S. Quelch. Mr. Quelch provided field notes prepared by Charles Bird on the joint collecting activities of Mr. Bird, James Chilcott, and Alexander B. Klots when they worked for the Canadian Northern Insect Survey in 1952 at Churchill. Those papers dealing with Churchill butterflies by the Chermocks (1968), Masters (1971), and Ferris (1975) have been drawn upon and acknowledgement of these sources is made here without subsequent mention.

Description of the Region

The specific area covered in this paper includes coastal tundra areas west of Christmas Lake Esker, west to Eskimo Point on the west bank of the Churchill River, and south to the vicinity of Warkworth Lake, which is situated in the taiga zone (Fig. 1).

Topography

The topography of the Churchill region has its origin in several geologic events. Over 600 million years ago, during the Precambrian Era, the Churchill quartzite was formed in an unstable basin known today as the Churchill region. Later, metamorphic pressures of the crust formed several geosynclines in this same area. Erosion reduced these geosynclines greatly and in the Ordovician period shallow seas laid down white dolomite muds and coral reefs upon the remaining geosynclinal ridges.

Pleistocene glaciation was the next geologic event that influenced the topography. Hudson Bay was formed from the melt waters of the retreating Wisconsin ice sheets. Additional waters from the south found their way to the early Hudson Bay by erosion of the geosynclines formed in the Precambrian past. The observer today finds the Churchill River flowing through such an erosion path. As ice retreated, planed off quartzite boulders along the bay have risen together with sand and gravel beaches, and glacial deposits of moraines and low eskers remain as major topographical features. Most of the soil is poorly drained and insulating permafrost remains as evidence of a colder past (Scoggan, 1959).

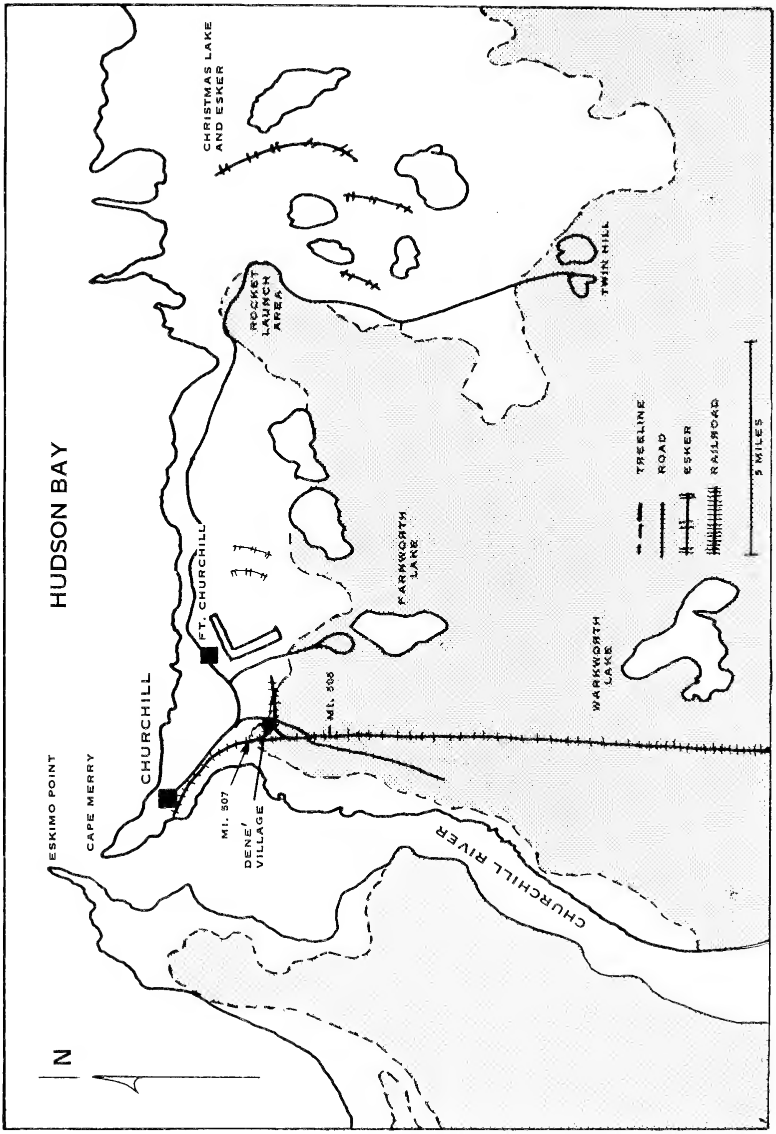

Figure 1. Map of the Churchill Region. Shaded portion represents the taiga biome.

Habitat Zonation

The Churchill region is very interesting from the standpoint of habitat zonation in that much of the region consists of an interface between two major terrestrial biomes, the tundra and the taiga. It is thus possible to observe the manner in which butterflies utilize this tension zone. Certain species may remain tied to their specific habitat requirements, be they climax tundra situations or closed spruce forests; others may exhibit a tolerance in the utilization of a broad range of habitats offered in the area.

Continental tundra reaches south to Churchill principally as a result of the cooling effect of Hudson Bay, the waters of which remain at near freezing temperatures even during the warmest parts of summer. A narrow belt approximating climatic conditions of the true arctic thus extends almost continuously around the south end of Hudson Bay, including most of coastal Manitoba, far northern coastal Ontario, and western coastal Quebec.

In the Churchill area there is a parallel zonation between treeline and the coast and, although irregular, treeline is generally 2-5 miles inland. "Treeline" is not always a clearly defined ecological feature; in many areas south of treeline are small patches of tundra, and north of treeline, notably in protection situations, it is not unusual to find areas of spruce and occasional tamarack. Ecological conditions of the true arctic are most closely approximated on exposed ridges in the area. In spite of variation in topography and vegetation at different sites, the following zones and dominant plants are generally present (Ritchie 1956; Scoffan 1959; and observations by the authors):

Zone	
1. Beach Meadow on Sandy Soil:	*Elymus arenaris, Carex maritima, Arenaria peploides.*
2. Coastal Flats:	*Puccinellia* spp., *Carex* spp., *Plantago maritima, Chrysanthemum arcticum.*
3. Coastal and Tundra Shrub Thicket on Ridges:	*Alnus crispa, Salix* spp., *Betula glandulosa.*
4. Heath and Heath-Meadow on Quartzite Outcrops and Rocky Beach Ridges:	*Juniperus communis* var. *depressa, Poa* spp., *Carex* spp., *Polygonum viviparum, Saxifraga tricuspidata, Dryas intergrifolia, Astragalus alpinus, Empetrum nigrum, Rhododendron lapponicum.*
5. Moss-Hummock Tundra on Wet Peat Flats:	*Sphagnum rubellum, Andromeda polifolia, Poa* spp., *Oxycoccus microcarpus.*

6. Sedge Meadow Tundra on Flooded Peat Flats:	*Eriophorum scheuchzeri, E. augustifolium, Carex* spp., *Scirpus caespitosus.*
7. Sedge Meadow Tundra on Dry Sand Flats:	*Carex* spp., *Poa arctica, P. glauca, Arctostaphylos rubra,* lichens.
8. Treeline Shrub Thicket:	*Betula glandulosa, Alnus crispa, Salix* spp., *Myrica gale, Ledum groenlandicum.*
9. Open Spruce-Tamarack Forest:	*Picea glauca, P. mariana, Larix laricina, Betula glandulosa, Cladonia alpestris.*
10. Closed Spruce Forest on Hummocky Peat:	*Picea mariana, Larix laricina, Habenaria hyperborea, Eriophorum vaginatum.*
11. Closed Spruce Forest on Elevated Flats and Ridges:	*Picea glauca, Ledum groenlandicum,* lichens.

In Figure 2 are illustrated diagramatically the relationships of the major plant communities, topographical features, and butterfly communities.

Resident butterfly species

Hesperia comma manitoba (Scudder) Collection Dates: 29 VI-20 VII

Distribution: Zone 10 principal; Zones 4, 8, 9, 11 occasional or rare.

Records available to the authors indicate that *H. comma* is strictly biennial in even-numbered years. It is highly sporadic in its occurrence; during most even-numbered years it is only occasionally encountered but during some it may be fairly common. The greatest proportion of specimens has been captured in areas south of treeline, especially in zone 10. Isolated captures are recorded in such diverse habitats as zones 4, 8, 9, and 11. In addition to the vicinity of Dene' Village, *comma* has been found near Warkworth Lake.

During 1974, this butterfly was relatively common in an area along the railroad tracks between Mile 505-507, including the spur track in the immediate vicinity of Dene' Village. During the period 7-15 July, 45 specimens were collected and many more observed. *Comma* was most often encountered on,or flying above, the crushed granite track bed. It is interesting to note that nearly half of the individuals collected were either in copula, or were netted during aerial mating maneuvers. Courting pairs were observed to ascend rapidly to a height of 30-40 feet, descend to near ground level, and then repeat the procedure up to several times. Upon completion of courtship behavior, mates either separated or began copulation.

Pyrgus centaureae freija (Warren) 17 VI-14 VII

Distribution: Zones 9, 10 principal; Zones 5, 8, 11 occasional or rare.

Pyrgus centaureae is a denizen of moist situations within the taiga zone. It is also occasionally found in moist treeline associated willow thickets and in closed spruce-tamarack forests on dry elevated places. It is sometimes encountered on the tundra, again in association with moist willow thickets.

This butterfly is only moderately common in collections of the Churchill area. It may be more frequent than collections indicate because of its difficulty to collect. *Centaureae* has a rapid darting flight and when it does alight, it generally does so only momentarily. The dappled light of a spruce forest and a grey-green sphagnum moss background contributes to its inconspicuous nature. *Centaureae* was not observed at flowers.

Pieris napi (Linnaeus) ssp. 16 VI-15 VII

Distribution: Zones 8, 9, 10 principal; Zones 3, 4, 5, 11 occasional or rare.

Napi can be found in nearly all moist tundra and taiga habitats but it is most common in zones 8, 9, and 10, particularly in association with willows. The authors noted this butterfly especially in wet willowy areas between Mile 505-507 of the railroad and along drainage courses on the tundra. Males were observed patrolling a broad area while females were noted in close association with willow thickets.

Colias hecla hela Strecker (T.L. Churchill) 21 VI-6 VIII

Distribution: Zone 4 principal; Zones 5, 6 occasional or rare.

Colias hecla is the rarest and most ecologically restricted species of its genus to be found in the region, being almost exclusively found in relatively lush tundra meadows on well-drained coastal or low tundra ridges. There have been a few captures additionally in sedge meadow situations on moist peat flats. The authors have found no records of this butterfly for the taiga zone. Ferris (1974, p. 257) misquotes Masters (1971, p. 8) when reporting the occurrence of *hecla* below treeline.

Churchill represents the southern end of *hecla's* distribution on the west coast of Hudson Bay and, judging from its rarity, its ecological requirements are only marginally met in the immediate Churchill-Fort Churchill area. It may well be more abundant on several ridges east of the Rocket Launching (Christmas Lake Esker and Knights Hill), where its habitat is extensive and virtually undisturbed.

As is the case with many arctic *Colias, hecla* has a strong and swift flight.

Colias gigantea gigantea Strecker 17 VI-14 VII

Distribution: Zones 3,5,6,8,9,10 principal; Zones 1,2,4,7,11 occasional or rare.

Gigantea is common and can be found in all habitat zones. It is, however, most abundant in moist areas where its foodplant *Salix reticulata* occurs. Klots (in Howe, 1975) reports observing this butterfly ovipositing on *S. reticulata* in late July at Churchill. Eggs were secured and larvae reared into third instar diapause in August.

In tundra environments with considerable relief, *gigantea* is most often encountered flying along ridge bases, at an interface between moist tundra flats and the ridge face. This interface area frequently affords a luxuriant growth of willows and numerous wild flowers; it, in many ways, resembles snowbed communities of the true arctic (see Porsild, 1964, p. 6). Oosting has observed similar flight behavior in *C. hecla* and *C. thula* (Hovanitz) on the North Slope and Seward Penninsula, Alaska. This topographical feature,in addition to providing a "flyway", affords some relief from the almost constant winds which characterize treeless regions.

A somewhat similar habitat is utilized by *gigantea* for patrolling flight in the taiga zone. Open linear areas within the spruce-tamarack forest (creek beds or the railroad right-of-way, for example) provide a "flyway". Both males and females appear to frequent these openings in equal numbers, although females tend to be much less active than males. When alarmed, *gigantea* exhibits its very strong and swift flight.

Gigantea is an avid flower visitor, being especially fond of the brightly colored reddish-purple and yellow flowers of *Pedicularis flammea* and *P. labradorica,* respectively. Individuals were also noted on *Chrysanthemum arcticum.*

Colias palaeno chippewa Edwards 24VII-13 VII

Distribution: Zones 3-6, 8-10 principal; Zones 1,2,7,11 occasional or rare.

This species is the most common and ubiquitous *Colias* in the region. It is most abundant in brushy areas where its food plant *Vaccinium (caespitosum* and perhaps *uliginosum)* occurs and it appears to reach maximum population densities in spruce-tamarack forests (zones 9 and 10). *Palaeno* uses open linear areas within the taiga for a flyway but, unlike *gigantea,* it seems to have less preference for the tundra flat/ridge base interface habitat.

The authors observed this species taking nectar from *Pedicularis flammea, P. labradorica, Chrysanthemum arcticum,* and the dandelion, *Taraxacum lacerum.*

Colias nastes moina Strecker (T.L. Churchill) 26 VI-13 VIII

Distribution: Zone 4 principal; Zones 1,2,3,5,7,8,9 occasional or rare.

Nastes experiences marked population fluctuations and is generally uncommon or rare in collections. Population densities affect the ecological distribution of this species. In years when population densities are at a maximum, there is expansion into normally unoccupied habitats; when population densities are low, "optimal" habitats appear to be utilized. During most years *nastes* is restricted to lush climax tundra meadows on well drained ridge tops and occasionally it is found in open spruce-tamarack forests, some 7-10 days prior to its emergence on the tundra. On rare occasions *nastes* can experience a "population explosion", being found in nearly every available habitat north of treeline, excepting very moist or permanently inundated tundra flats.

During 1974, the authors located a very large colony of this species immediately north of Churchill (Windy Point). Over 300 specimens were collected in less than 7 hours during the period 18-20 July, with no apparent effect on population densities.

Nastes is an active butterfly; both sexes can be observed taking nectar from flowers, including *Oxytropis campestris, Astragalus alpinus* and *eucosmus, Hedysarum mackenziae,* and *Saxifraga caespitosa.* Females are somewhat less active than males, being found in association with the larval foodplant *O. campestris* (see Klots in Howe, 1975). Males typically patrol a broad area, pausing occasionally to obtain nectar.

This species exhibited a behavior not noted in other butterflies of the region, that of remaining active until shortly before sunset. On July 18 in particular, individuals were noted to be on the wing until 9:00 P.M. (CDT). This behavior was again observed on the 19th and 20th. Temperatures on all days (July 18-20) remained at a rather balmy 60-70°F, no doubt contributing to this unusually prolonged activity.

Plebejus optilete yukona (Holland) 9-5 VII

Distribution: Zone 10 principal; Zones 9, 11 occasional or rare.

This species was first collected at Churchill by Ferris in 1973 (Ferris, 1974) and it has since established itself in principally closed spruce forests from approximately Mile 505-507, including the area along the spur track south of Dene' Village. It is difficult to imagine that *optilete* has, until recently, been overlooked by collectors. This leads one to assume that it is an introduction from farther south, perhaps via the railroad from Gillum.

Optilete has a weak flight and seems to seek sunlit openings within the forest, particularly saturated mud along road and creek banks. The authors have found *optilete* to behave similarly in the Yukon and central Alaska.

Plebejus aquilo lacustris Freeman 26 VI-19 VII

Distribution: Zone 4 principal; Zone 7 occasional or rare.

Aquilo is uncommon to rare in collections of the Churchill region.

Records available to the authors indicate that it is restricted to dry tundra meadows on the rocky ridges between Fort Churchill and Eskimo Point. *Aquilo* may be frequent at times but its small size and light grey ventral scaling render it highly inconspicuous when it is resting on a grey lichen-covered rock or on a grey-green tundra meadow background. *Aquilo* generally flies close to the ground and can be very difficult to follow visually when alarmed.

Most individuals are encountered in very dry, rock strewn meadows; occasionally this species is observed at moist sand. One male was observed taking nectar from *Parnassia kotzebuei.*

Glaucopsyche lygdamus (Doubleday) ssp. 22 VI-15 VII

Distribution: Zones 4, 9, 10, 11 occasional; principal zone undetermined.

The authors collected 2 males and 4 females of this poorly known member of Churchill's fauna. *Lygdamus,* along with *Boloria freija* (Thunberg) and *Erebia rossii ornata* Leussler, is the first species on the wing in June. Two freshly emerged males were collected on 22 June in the vicinity of Mile 505. Two additional specimens were captured in the taiga zone, one female was taken at Mile 507 on 25 June and another female was found on 15 July at the same location. Parshall secured an additional female on 26 June in a dry treeline situation SE of Fort Churchill.

Oosting noted a female at Cape Merry, also on the 23rd of June. This individual was observed sunning itself on a black lichen-covered rock at approximately 7:30 PM (CDT). It appeared to be very lethargic and flew to another spot only when closely approached. After reaching a "safe distance", a sun-oriented position, with wings open against the rock, was again assumed.

Boloria frigga saga (Staudinger) 17 VI-1 VIII

Distribution: Zones 3,5,8,9,10 principal; Zones 1,2,4,6,7,11 occasional or rare.

This is the most common *Boloria* in the region and is nearly ubiquitous in its distribution. Maximum abundance is realized in wet willowy areas in both tundra and taiga situations. Males of this species frequently patrol willow thickets while females remain somewhat less active. Both sexes visit flowers on occasion, particularly the pink flowers of *Rubus arcticus.*

Boloria polaris stellata Masters (T. L. Churchill) 20 VI-28 VII

Distribution: Zones 5, 6, 7 principal; Zones 2, 3, 4, 8, 9 occasional or rare.

Polaris is another species of the true arctic whose southern most collecting station on the west coast of Hudson Bay is in the Churchill area. This butterfly is most often collected on moist tundra flats.

All published records for this species have been from odd-numbered years and the authors failed to find this species in 1974, as expected. John Ebner *(in litt.)* reports, however, that he has received specimens from Churchill which were collected on even-numbered years (1968 & 1970). While *polaris* does not then appear to be strictly biennial in odd-numbered years, there are at least very pronounced odd-even year fluctuations.

Boloria freija (Thunberg) ssp. 10 VI-15 VII

Distribution: Zones 9, 10, 11 principal; Zones 1-5, 7, 8 occasional or rare.

When spring finally comes to the forested areas south of Churchill, in early to mid-June, *freija* begins full emergence. The authors were amazed at how abruptly the flight season begins at Churchill; particularly was this noted in regard to *freija.* When the authors first arrived on 20 June, the taiga was devoid of butterflies. One specimen of *freija* was taken on 21 June after a full day in the field under sunny skies, and on 22 June nearly 100 specimens were collected in 3 hours. The peak flight period of *freija* appears to last less than one week in the taiga zone.

This species is rather uncommon in collections of the area, probably because most collectors arrive after its principal flight in the taiga zone. Although *freija* is distributed in all but permanently inundated *Eriophorum* flats, it is only abundant south of treeline. Within zone 9 *freija* is generally distributed, while in closed forests it frequents sunlit openings. *Freija* is uncommon in dry tundra sites and only occasional in other tundra environments.

A large concentration of *freija* was found on the elevated peat-covered moraine, immediately east of Mile 505. The ridge top is largely open (disturbed) spruce forest with a ground cover of the depressed and much branched Bilberry, *Vaccinium caespitosum.* Females of *freija* were observed fluttering over this plant and close observation revealed that the *Vaccinium* was indeed being utilized as an oviposition substrate. On dry tundra flats, females of *freija* were observed flying slowly over the matted Bearberries, *Arctostaphylos rubra* and *alpina;* these individuals were not observed ovipositing, however. *Vaccinium caespitosum* has not been demonstrated to be the larval foodplant of *freija* in the Churchill region, but it should be strongly suspected as such.

Boloria titania boisduvalii (Duponchel) 1 VII-9 VIII

Distribution: Zones 3, 8, 9, 10 principal; Zones 2, 4, 5, 6, 11 occasional or rare.

After other *Boloria* have passed peak abundance, *titania* becomes the most noticeable member of its genus to be found in both tundra and taiga environments. Like its relatives, *titania* is widely distributed in the region. The authors found this species to be most common along the flowery right-of-way of the railroad, particularly in the vicinity of Dene' Village.

Boloria eunomia triclaris (Hubner) 23 VI-9 VIII

Distribution: Zones 3, 8-10 principal; Zones 1, 2, 4-7, 11 occasional or rare.

Boloria eunomia can be found in all habitats offered in the region but is most common in zones 8, 9, and 10, especially along the railroad right-of-way. Moist willowny areas at the base of elevated ridges also support good colonies of this butterfly.

Both sexes visit flowers avidly. Nectar sources include *Ledum decumbens, Loiseleuria procumbens, Dryas intergrifolia, Rubus arcticus, Taraxacum lacerum,* and *Chrysanthemum arcticum.*

Oeneis taygete taygete Geyer 26 VI-15 VII

Distribution: Zones 4, 5/7 principal.

Oeneis taygete has been variously reported from Churchill in the past and, while there are undoubtedly valid specimens, most records appear to be based on misdetermined specimens of *Oeneis polixenes* (Fabricius). In 1974 the authors collected specimens which were tentatively identified as *taygete;* subsequent genitalic dissections proved them to be this species and, although variable, Churchill specimens agree very well with material from Fort Chimo, Quebec, both in facies and in genitalic characters.

All of the individuals encountered during the 1974 season were collected in moist tundra meadows, particularly on the south-facing slopes of the rocky ridge immediately east of Fort Churchill. *Taygete* was also found to frequent moist grassy margins of dry sand flats (low eskers) in an area approximately 1 mile east of the above-mentioned ridge.

Taygete, like its relatives *Oeneis polixenes* and *O. melissa semplei* Holland, is difficult to capture when alarmed. All three species are observed to orient their bodies in a manner which minimizes the shadow cast by the sun —an action which, in combination with their cryptic coloration, makes these animals much less visible to predators.

Oeneis jutta (Hubner) ssp. 20 VI-15 VII

Distribution: Zones 5 (in association with spruce), 9, 10 principal; Zones 6, 8 occasional or rare.

Masters (1971) proposes the existence of two subspecies of *O. jutta* in the region. *O. jutta alaskensis* Holland supposedly flies principally in even-numbered years and is found in to wet tundra habitats. *O. jutta ridingiana* Chermock & Chermock, he asserts, is a denizen of the taiga zone, perhaps occurring on the tundra in association with clumps of spruce. This subspecies is to be found in principally odd-numbered years. It is further suggested that the odd and even year populations differ in phenotypic characteristics.

During 1974 the authors found *jutta* only in the taiga zone, particularly in association with hummocky black spruce forests (zones 9 & 10). Although suitable tundra habitats were checked for this species, no individuals were encountered. Collecting records available to the authors from other even-numbered years (particularly those of Klots, Bird, and Chilcott, 1952) indicate a taiga zone or treeline distribution for *jutta.* These data seriously conflict with the model proposed by Masters and, while by no means conclusive, they point out the need for a careful study of the situation.

Oeneis melissa semplei Holland 12 VI-2 VIII

Distribution: Zones 4, 7 principal; Zones 1, 2, 5, 9 occasional or rare.

Melissa has rather restricted habitat requirements, occurring principally in dry tundra meadows. The authors found this species to frequent particularly the dry meadows on low sandy eskers which are occasional on tundra peat flats in the region (a low esker generally rises some 3-5 ft. above the tundra flats). Dry ridge-top meadows likewise provide a principal habitat for *melissa.*

A low esker formation on the peat flats 1 mile SE of Fort Churchill was found to support a good colony of this species. Individuals of *melissa* exhibited a marked preference for the dry meadow on this sand formation; when alarmed, some individuals would fly a short distance onto wet peat tundra but in a short while they would again return to the dry meadow habitat. On windy days, *melissa* appeared to confine its flight activities to the protected lee side of the esker formations.

Melissa, like other *Oeneis,* was not observed at flowers.

Oeneis polixenes polixenes (Fabricius) 12 VI-2 VIII

Distribution: Zones 3-6, 9 principal; Zones 1, 2, 7, 8 occasional or rare.

Oeneis polixenes is the most common and widespread member of its genus. It can be observed in every tundra habitat but is most abundant in moist areas. Wet, open spruce-tamarack forests at and somewhat south of treeline also support good numbers of this species.

The Churchill population of *polixenes* displays a great deal of phenotypic variation. There appear to be two principal phenotypes, and there is a spectrum of variation in between. Some specimens appear typically ruddy brown; others are much paler grey-brown above and their ventral secondaries often show veins outlined in grey. The latter phenotype resembles *O. taygete* (and is much confused with it), but it is genitalically similar to *polixenes.* Careful study will be required to determine whether this variation is entirely individual or whether there are two sibling species involved.

Erebia rossii ornata Leussler (T.L. Churchill) 10 VI-19 VII

Distribution: Zones 5, 6, 9 principal; Zones 1-4, 7, 8 occasional or rare.

Among the *Erebia, rossii* is the most abundant and widespread species. Although recorded from all tundra environments, it reaches maximum population densities in wet habitats, including treeline situations where there are wet tundra openings. *Rossii* is the earliest recorded species in the region, but its emergence probably lags behind that of *B. freija* in the taiga zone by a few days.

Erebia disa mancinus Doubleday 25 VI-15 VII

Distribution: Zone 10 principal.

This species appears to be a recent addition to Churchill's fauna. *Disa* was first collected by Ferris in 1973 (one pair) (Ferris, 1974) and in 1974 it was found commonly in closed spruce forests south and somewhat southwest from the railroad switchback area. While collectors may have overlooked this butterfly in the past, it seems more likely that *disa* has been introduced from some point south along the railroad.

Disa has among the most restricted habitat requirements of any butterfly in the region. It is found only in moist, hummocky, closed spruce forests (muskegs). *Disa* occasionally ventures into sunlit openings, but generally it remains within its shaded forest habitat. This species presents a challenge to the collector, for when alarmed, *disa* flies rapidly through even the densest part of the muskeg, virtually disappearing in shadows.

Erebia discoidalis discoidalis (Kirby) 15 VI-10 VII

Distribution: Zones 8-10 principal; Zones 5, 6, 11 occasional or rare.

Erebia discoidalis is only moderately common and it appears to prefer moist, boggy situations at and south of treeline. Occasional specimens are taken on wet tundra flats. The authors found this species in particular numbers north of Farnworth Lake.

Discoidalis and *E. disa* were not observed to be on the wing during late afternoon or early dusk; instead they choose the warmest part of the day (10:00 AM-3:30 PM, CDT) for activity.

Erebia theano canadensis Warren (T.L. Churchill) 2-24 VII

Distribution: Zones 3, 4 principal; Zones 1, 2, 5, 9 occasional or rare.

This poorly known member of Churchill's butterfly fauna is extremely local. *Theano* experiences pronounced population fluctuations; in some years it is very rare, in other years it may be uncommon, and in exceptional years it can be locally abundant. The latter was the case in 1974 when, on the 18th and 19th of July, the authors collected nearly 150 specimens and observed many more. The Chermocks found it locally uncommon in the

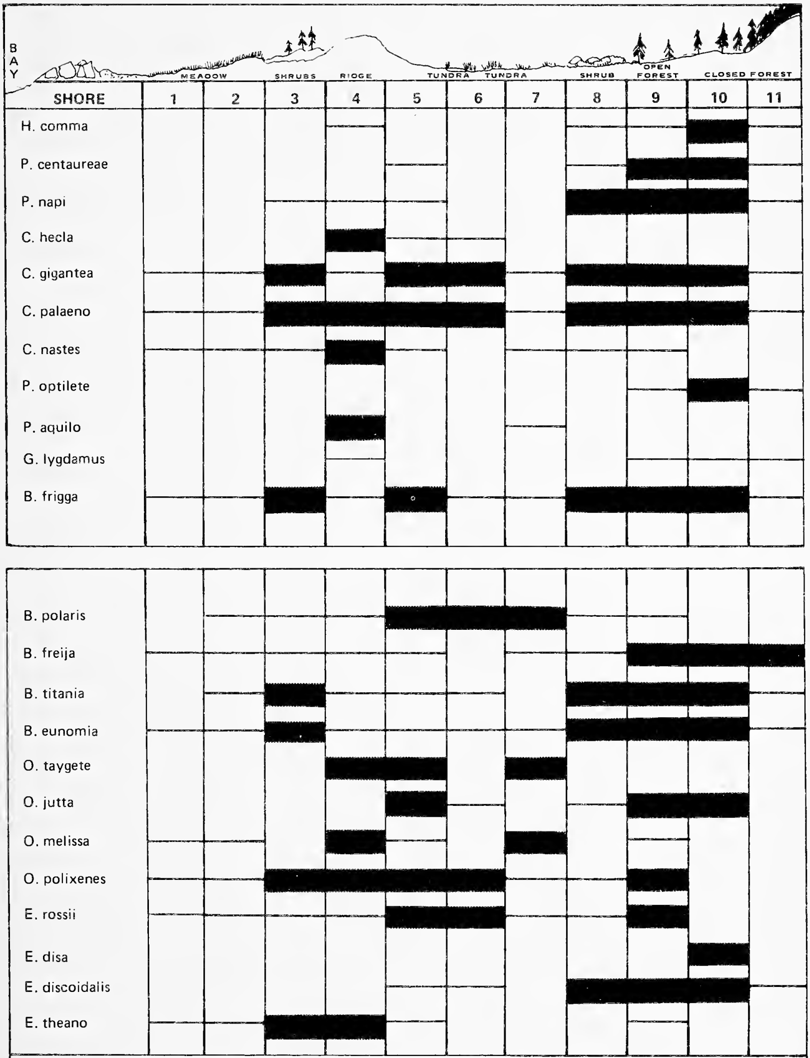

FIG. 2 Diagram illustrating the zonation of resident butterflies in relation to vegetation and topography in the Churchill Region. Shaded bars represent the principal habitat zone(s) occupied by each species; lines represent occasional or rare occurrence therein.

early sixties and Ferris found several scattered colonies in 1973. Bird, Chilcott, and Klots intensively collected the region in 1952, but found only 5 specimens. John Ebner's collector failed to find it during three successive seasons in the mid-sixties.

Theano is most widely distributed on the tundra, being found especially in very luxurient, flowery meadows. Colonies have been reported from widely scattered locations, including Fort Prince of Wales (Eskimo Point), the area about H.M.C.S. Churchill, and on the grassy ridges near Fort Churchill. The authors found *theano* to be concentrated in the lush ridgetop meadows immediately northwest of Churchill (Windy Point) during 1974. Its distribution also includes the taiga zone, where it occasionally appears in grassy openings, particularly near Mile 505 and 506.5 (switchback area).

On the tundra, *theano* is observed to be an active butterfly and, in spite of its weak flight, it moves widely within the confines of its meadow habitat. Males are most active, while females spend much time within low willow thickets which border the meadow. Both sexes are observed at flowers, notably those of *Astragalus* ssp., *Oxytropis* ssp., and *Antennaria rosea.* When alarmed, *theano* generally retreats to concealing willow thickets. In the presence of even moderate winds, individuals choose not to fly but instead seek wind sheltered spots.

Other species

The foregoing has dealt with those butterflies which the authors regard as permanent breeding residents of the Churchill region. A substantial number of other species has been recorded from the area. Some are strays or casuals, others may be repeated migrants, and several may be permanent residents which occur in very small numbers. They include: *Papilio glaucus canadensis* Rothschild & Jordan, *Pieris protodice* Boisduval & Le Conte (the occurrence of this species was confirmed when Parshall captured one female on 9 July 1974 near a pile of grain along the railroad), *P. rapae* (Linnaeus), *Colias eurytheme* Boisduval, *Lycaena helloides* (Boisduval)/*L. dorcas* Kirby complex, *Lycaeides argyrognomen scudderii* (Edwards), *Vanessa atalanta* (Linnaeus), *V. cardui* (Linnaeus), *Nymphalis milberti* (Godart), *N. antiopa* (Linnaeus), and *Boloria selene* (Denis & Schiffermuller) ssp.. Masters (1971) or Ferris (1974) can be consulted for details in regard to these species.

The authors collected one additional species not before recorded from the area, *Everes amyntula* (Boisduval). One somewhat worn female was captured by Parshall on 11 July near Dene' Village, and one fresh male was taken by Oosting on 19 July near Windy Point. This species is tentatively regarded as a nonresident, perhaps having found its way to Churchill by railroad.

Summary

With respect to habitat zonation, there are essentially five groups of species to be found in the Churchill region. These species are: (1) exclusively restricted to climax tundra habitats (*C. hecla, P. aquilo,* and *O. taygete),* (2) essentially arctic or arctic-alpine in distribution but which can utilize tundra-taiga ecotone or taiga habitats *(C. nastes, B. polaris, O. melissa, O. polixenes, E. rossii,* and *E. theano),* (3) species whose distribution is not correlated with treeline *(P. napi, C. gigantea, C. palaeno, G. lygdamus, B. frigga, B. freija, B. titania,* and *B. eunomia)*, (4) primarily distributed in the taiga or boreal forest biomes but can utilize taiga-tundra ecotone or tundra habitats *(H. comma, P. centaureae, O. jutta,* and *E. discoidalis),* and (5) exclusively restricted to taiga zone environments *(V. optilete* and *E. disa).* Notes have also been made on spatial distribution, adult behavior, biology, and nectar source preferences.

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Habitat: *Lycaena heteronea clara* (Lepidoptera: Lycaenidae)

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The Southern California butterfly *Lycaena heteronea clara* Henry Edwards, illustrated on the cover of this issue, has a rather restricted distribution in Kern, Ventura, and Los Angeles Counties, from the Mount Pinos area east to the Tehachapi Mountains, with isolated records to the north (Piute Peak) and south (Silverwood Lake area, San Bernardino Mountains) Orsak, L.J., 1977, Management recommendations for populations of the Bright Blue Copper Butterfly (*Lycaena heteronea clara*) of Southern California. *Atala* 4 (1-2): 10-18. ("1976"). Within this range, *clara* occurs in discrete colonies, often greatly isolated from one another; therefore it has been rarely collected. Although rareness is often associated with extreme specialization, *clara* inhabits a fairly wide elevational span and utilizes three *Eriogonum* species (Polygonaceae) as larval foodplants. The presence of abundant food-plant, however, does not necessarily indicate the presence of *clara*; foodplant quality is also important (Orsak op. cit).

In O'Neil Canyon (figure 1) and adjacent large canyons near Lebec, *clara* inhabits flat areas ranging from 3000-4750 feet (917-1452 meters) in altitude where *Eriogonum fasciculatum* var. *polifolium* (Bentham) Stokes is present and often dominant among scattered *Quercus lobata* Nee trees.

At the east end of Frazier Park (figure 2) and other sites throughout Cuddy and Lockwood Valleys at elevations from 3950-5400 feet (1208-1651 meters), *clara* inhabits the juniper-Pinon Woodland Community of Vasek and Thorne, Vasek, F. C. and R.F. Thorne (1977 Transmontane coniferous vegetation. pp. 797-832 in Barbour, M.G. and J. Major (eds.), *Terrestrial Vegetation of California.* Wiley-Interscience). *Eriogonum fasciculatum* is common among the dominant shrubs *Artemisia tridentata* Nuttall and *Chrysothamnus nauseosus* (Pallas) Britton, and the occasional trees *Pinus monophylla* Torrey & Fremont and *Quercus chrysolepis* Leiberg. Many such colonies are adjacent to or within dry washes, where females preferentially oviposit on *Eriogonum heermanii* Durand and Hilgard.

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Fig. 1. O'Neil Canyon, near Lebec, Kern County, California.

Fig. 2. East end of Frazier Park, Kern County, California.

Fig. 3 Northwest slope of Frazier Mountain, elevation 6750 feet, Ventura County, California.

Near the summit of Frazier Mountain (figure 3), and at many locations in Lockwood Valley, at elevations between 5200-7900 feet (1606-2431 meters), *clara* colonies utilize *Eriogonum umbellatum* var. *munzii* Reveal as larval foodplant. At lower elevations, hillside clearings in forests of *Pinus monophylla* are inhabited, while colonies at higher elevations occur in rocky outcrop openings in Yellow Pine forest (*Pinus ponderosa* Lawson; *Pinus jeffreyi* Greville & Balfour).

Journal of Research on the Lepidoptera 17(3):207-208, 1978(80)

Book Review

A Compendium of the Biographical Literature on Deceased Entomologists
Pamela Gilbert. 1977. 452 pages, frontispiece and 27 small portraits. British Museum (Natural History), Cromwell Road, London SW75BD, England. Price: 25 British Pounds (ca. $60 U.S.)

This book is a very useful expansion of M. M. Carpenter's "Bibliography of Biographies of Entomologists" *Amer. Midl. Nat.* 33: 1-116, 1945 and 50: 257-348, 1953). Gilbert's compendium contains references to biographical information on some 7,500 deceased entomologists. References up to the end of 1975 are included. An entomologist is considered to be anyone who has published on insects (although some others, such as early collectors, are included). The names are arranged in a neat and easy to use format. The book is a must for anyone interested in historical information on entomologists.

The compendium appears quite complete, and major entomological journals are well covered. The following are among the few omitted references to lepidopterist: **T. D. A. Cockerell** (by W. A. Webber, 1965, *Univ. Colo. Studies, Ser. Bibliog. 1: 1-124),* **J. A. Comstock** (1963, *J. Res. Lepid. 2: 204* and by L. M. Martin, 1972 *Bull. So. Calif. Acad. Sci. 71: 57-60),* **R. M. Fox** (1965, *J. Res. Lepid. 4: 251),* **F. Grinnel, Jr.** (by J. A. Comstock, 1975, *J. Res. Lepid. 14: 90-91),* **E. Piazza** (by E. P. Van Duzee, 1926, *Pan-Pac. Ent. 2: 160* and by J. A. Comstock, 1975, *J. Res. Lepid. 14: 90),* **J. J. Rivers** (by F. Grinnell, Jr., 1914, *Bull. So. Calif. Acad. Sci. 13: 16-17* and *Pom. Coll. J. Ent. & Zool. 6: 98-1100),* **W. Schrader** (1933, *Bull. So. Calif. Acad. Sci. 32: 39-40),* **W. G. Wright** (by J. A. Comstock, 1975, *J. Res. Lepid. 14: 92* and by F. Grinnell, Jr., 1913, *Bull. So. Calif. Acad. Sci. 12: 19-21),* and **W. S. Wright** (1933, *Bull. So. Calif. Acad. Sci. 32: 129* and by J. A. Comstock, 1975, *J. Res. Lepid. 14: 91-92).* Also not included are the many references to lepidopterists in J. Ewan's "San Frncisco as a mecca for nineteenth century naturalists" (pages 1-63 in *A Century of Progress in theNatural Sciences,* California Academy of Sciences, 1955). Additional omitted biographies (of non-lepidopterists) are noted in a review of the compendium by A. B. Gurney (*Bull. Ent. Soc. Amer. 24: 443, 1978).* For lepidopterists, an important supplement to the compendium is *The Lepidopterists' Society Commemorative Volume,* compiled by R. O. Kendall and published in 1977 by the Lepidopterists' Society.

Gilbert's compendium is a major contribution to the study of the history of entomology and entomologists. It is unfortunate though, that the high price (especially considering that the illustrations are limited to four pages of black and white photographs) will limit its availability.

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Artificial Diets for Insects, Mites, and Spiders
Pritam Singh. 1977. 595 pages. IFI/Plenum, New York, Washington, & London. Price: $75.00

In recent years many research programs devoted to insect physiology, ecology and genetics have made use of artificial diets for rearing insects, and such procedures are used routinely to develop insect control techniques. The literature on this subject is, therefore, voluminous and Singh has performed a great service to workers by bringing together some 2000 references into one readily accessible volume.

The introduction contains a useful section on formulation of diets which outlines the importance of texture, water content and shape as well as nutrient balance and phagostimulants. There is also a brief note concerning evaluation of diets, containing examples of data sheets employed in the author's laboratory which can be readily adapted to meet most requirements.

The bulk of the work consists of abstracts of publications on artificial dietrs taken from over 100 journals and periodicals covering the period from 1900 to the beginning of 1976. Where possible, the format used for each abstract consists of the reference, composition of diet, methods of preparation, details of rearing conditions and data on development. Singh's approach has served to emphasize the inadequate nature of many of the original publications, since often data for one or more of these categories are incomplete or missing. It would be helpful if Singh's format could be kept in mind by those publishing in this field, since the success of a diet often depends on techniques and procedures used in the preparation and methods of handling the insects. The author does, however, warn that some details may have been lost in condensing the paper and it is therefore advisable to refer to the original publication before making a diet.

In addition to some general purpose and commercial formulations, the groups covered are: Coleoptera, Dictyoptera, Diptera, Hemiptera, Isoptera, Lepidoptera, Neuroptera, Orthoptera, Siphonaptera, Acarina and Araneida. The work concludes with an Appendix, containing the composition of commonly used salt and vitamin mixtures, and an extensive bibliography.

Although Singh has succeeded in his aim to give complete, but concise, coverage of existing knowledge of insect dietetics, it is perhaps a little disappointing that he deliberately made no attempt to explain, criticize or otherwise evaluate the performances of the diets listed. A brief examination will show that many diets have been improved and the retention of the original in a volume of this type is only of historical interest unless comparison with the later forms shows which factors have produced the improvements. However, the data are herein readily available to enable other workers to perform such evaluations.

The volume will be appreciated by professional workers as a valuable summary, although most probably already have, or have access to, many of the original publications to which Singh refers. Those just embarking on projects using artificial diet techniques will also find the work useful, but would benefit from more detailed section on evaluation and preparation of diets and rearing techniques. The book may also be of great value to amateur entomologists who wish to rear insects as part of their general interest in the field or as part of experimental programs. Unfortunately, many are likely to find the price prohibitive, particularly as it does not reflect the quality of type or binding.

Singh has produced a valuable compendium of diets. It would now be an even greater contribution if he would consider producing a smaller, cheaper volume containing only the most successful diets together with evaluations and general comment about the principles of formulation of artificial diets. He is clearly well qualified to do so.

Ashley C. Morton, Walthamstow Hall, Sevenoaks, Kent, England.

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Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbrevations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

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Review: All papers will be read by the editor(s) & submitted for formal review to two referees. Authors are welcome to suggest reviewers, and if received, submit name & comments of reviewers.

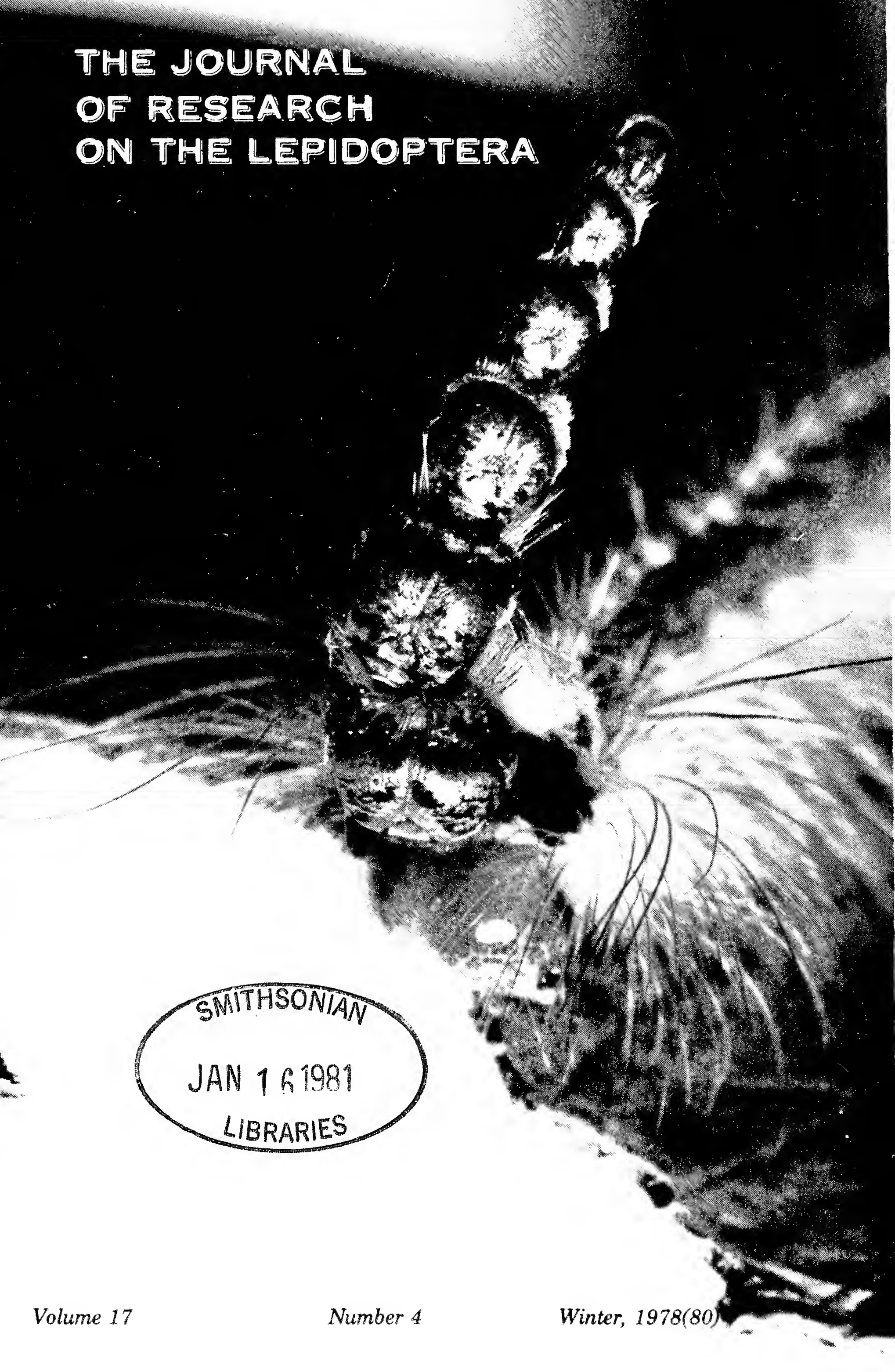
THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Volume 17 *Number 3* *Autumn, 1978(80)*

IN THIS ISSUE

Cover Illustration: *Lycaena heteronea clara* female necturing on *Eriogonum fasiculatum.*

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA



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Retention of Cast Head Capsules by Some Nolid Immatures in Four Old World Countries

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Abstract. Certain unique features of the developmental stages of the Australian nolid *Uraba lugens* are described and illustrated, including the retention of cast head capsules by each succeeding larval instar. In many individuals this stack remains intact through pupation where several capsules remained to decorate the cocoon. Earlier observations of the same phenomemon are cited, including *Rhynchopala argentalis* in India, *Roeselia togatulalis* and *R. nitida* in Europe, and *Mimerastria mandshuriana* in Japan. These five cases in four distinct areas of the Old World, are the only so far observed amongst the nolid moths.

Uraba lugens Walker (1863), the AUSTRALIAN nolid moth illustrated here, has been variously referred to *Coesa, Mosoda, Nola, Roeselia, Sorocostia, Toxoloma,* and *Uraba.* D. S. Fletcher of the British Museum (Nat. Hist.) has informed me (in litt. - 1972) that it is probably best placed in *Uraba*; that *lugens* is the type species of *Uraba,* that a synonym of *U. lugens* is *Coesa viduella* Walk. (with the Tasmanian type specimens of both in the B.M.), and that *Roeselia* is a generic synonym of *Nola,* to which latter genus *lugens* is certainly not referrable. Its common name is the gum-leaf skeletonizer moth (Campbell, 1962).

In most years this moth is extremely abundant in the vicinity of Blackwood, South Australia (a southern suburb of Adelaide), in the foothills of the Mt. Lofty Range at about 900 feet elevation. The larvae skeletonize, and sometimes nearly defoliate, various *Eucalyptus* spp. (gum trees — MYRTACEAE) in many localities across southern and eastern Australia. They are highly gregarious in the early instars, feeding closely side by side, but gradually become semi-gregarious to more-or-less solitary as they mature. There are eleven instars according to Campbell (1962). The larvae rest exposed on, or near, the areas of feeding and are easily discovered by searching. They are able to cling with great tenacity to the flat surfaces of the smooth eucalypt leaves, with no need for silken mats or other aids to attachment, although a slight silk mat is woven for anchorage prior to moults. The major foodplant at Blackwood is *E. odorata* Behr ex Schldl. (peppermint box or mallee box); mature and tough older leaves seem to be preferred. The same moth, or possibly a subspecies, also occurs in the SW. of Western Australia, ranging at least as far north as Geraldton, where it can be abundant. Around Geraldton, they are often conspicuous on *E. camaldulensis* Dehnh. in March and on other eucalypts of the city streets and gardens.

The primary purpose of this paper is to illustrate, with photographs, the bizarre way in which a series of cast larval head capsules are transported about, in the form of a cephalic "horn", by the larvae of *U. lugens* (Figs. 6-10). This retention and transport of cast head capsules is a morphological phenomenon which is maintained automatically with each successive moult, after the 4th or 5th instar, as an end result of the manner in which the prothoracic or cervical portion of the most recently-moulted skin (with its associated hair tuft still intact) remains securely attached to the next (earlier) head capsule above it. This erect or curving column of cast head capsules is in no way tied together or otherwise held in place by means of silk as might at first be suspected. (An observer from the United States might notice the amusing similarity of this tapering stack of head capsules to the caudal appendage of a rattlesnake — *Crotalus* sp.!)

It is hard to imagine what (if any) purpose the retention of a stack of head capsules might serve. Perhaps it might attract the first one or two investigative pecks from a bird or lizard; the predator would initially obtain only a mouthful of dry exuviae. However, the dense, hairy coat alone (consisting of both short, bristle-like and more elongate, softer setae) would probably serve as an adequate repellent for most birds. If a bird really desired to consume one of these larvae, it is unlikely that it would be deterred by a stack of rather easily-dislodged exuviae attached to one end of the morsel.

These stacks of head capsules are sometimes dislodged, altogether or partially, under natural conditions, but I have never observed such "hornless" larvae showing signs of injury or any abnormal behavior. The capsules could be lost accidentally at times -- for example, by being dislodged when a larva crawls through a narrow passage between leaves or twigs, or during strong winds and rainstorms, conditions which can be relatively frequent during winter. Mature larvae, with complete sets of head capsules intact, are often encountered under natural conditions. (Fig. 9 shows a mature larva carrying a complete set, as viewed from the front; it had been feeding at the leaf edge before the photo was taken.)

I have never observed these larvae in the process of moulting. In this particular case, close observation of the moulting procedure could be of some interest. Note how the long anterior setae of the thoracic region sweep forward and upward into (behind) the two most recent capsules, thus stabilizing the whole stack over the head of the living larva (Fig. 6). The degree to which the tip of a complete stack sometimes curves back is shown in Fig. 8; in earlier instars, the head capsule "horn" is relatively straight and usually somewhat forward-directed, or it can be nearly vertical. The larva in Fig. 7 is depicted in a typical resting position on a stem of *Eucalyptus odorata*.

As a unique signature to this distinctive larval habit, the head capsule stack (or, more often, a part thereof) is usually attached to the outside of the cocoon, positioned centrally (Fig. 10). Some cocoons observed did not have any head capsules attached, but many did. I do not recall ever having seen a cocoon that was decorated with more than 3 or 4 head capsules, although I was not studying this species intensively during my years at Blackwood. These notes are drawn only from one complete rearing, supplemented by various casual field observations. I won't even attempt to speculate on possible "reasons" why these larvae should attach their cast head capsules to their cocoons! If anything, one would think that this might tend to make an otherwise well-camouflaged cocoon somewhat easier for potential enemies to discover.

The construction of one cocoon was observed. I am quoting below from my field notebook (N1.2, in part):

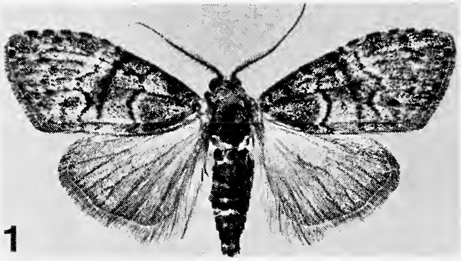
"In a typical nolid cocoon, elongate and spindle-shaped; formed on a stem of the foodplant, from which slivers and particles of epidermis or thin bark are chewed and then woven (from the inside) into the structure, the end result blending nicely into the contour of the stem to which it is attached. The cocoon is started by building up both sides, "boat-like", as the larva chews material off the stem upon which it clings outstretched, and (later) from just to the front and rear of the cocoon limits. Most of the thin bark particles chewed from the stem are fairly long and splinter-like; they are built into the cocoon walls roughly parallel to each other and are horizontally placed. The silk is fairly tough and paper-like; color pale tan in the finished cocoon........The pupa fits very snugly inside, and great care must be taken not to injure it if attempting to open the cocoon......" (The latter is also a typical nolid phenomenon.)

Campbell (1962) states that the majority of cocoons are formed under bark, lower down on the trunks, or in leaf litter on the ground.

The pupa is a rich, medium-brown in color, shading to very dark brown on the dorsum, especially in the thoracic region, with a dark brown line on the dorsomeson. Shell rather soft, with very little surface gloss. Abdominal movement was noted as being "lively, but only within a rather restricted circle, quick and spasmodic, then stopping abruptly."

The lowland-coastal form of this moth is further characterized by its most distinctive mode of oviposition: The eggs are securely-glued (with a nearly colorless adhesive) to the relatively smooth, flat surface of a living eucalypt leaf, in precisely-shaped parallel rows. Fig. 5 (left) shows a close-up of only a few eggs in one oviposition. For a more complete picture of one egg "mass", see McFarland (1972: 229, Fig. 17); a photograph depicts nearly all the eggs in one female's oviposition — in that particular example, consisting of seven parallel rows, each containing between 17-22 eggs (total of about 135 eggs). Some ovipositions observed contained as many as 8 to 10 parallel rows and more than 180 eggs. A straight row containing 18 eggs in close contact measured 9 mm. in length. A most distinctive (possibly unique) feature of larval emergence from the egg is that no chewing of the shell takes place. Instead, a round and clean-cut preformed operculum or "lid" is pushed off the top of the egg by the emerging larva. Fig. 5 (right) shows two S.E.M. photos depicting empty (hatched) egg shells of *U. lugens,* with opercula ajar. In many cases, the lids fall away altogether after the larvae depart, but sometimes they fall back into the opening or remain balanced a little to one side. This is reminiscent of many hemipterous eggs, but I have never before observed this mode of eclosion in any other species of Macrolepidoptera. Larval silk strands can be seen on some of the eggs. No post-eclosion feeding on the empty egg shells takes place in this species.

The photographs of adults included here (Figs. 1-4) compare well with the *lugens* series in the B.M.N.H.. The adults are strictly nocturnal, coming in abundance to ultraviolet light. There are two generations per year at Blackwood: a spring-early summer brood is on the wing from late Oct.-Dec., and a late summer-autumn brood flies from late Feb.-April.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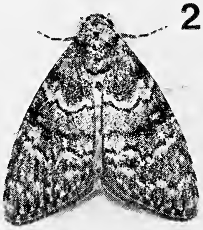
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Figs. 1 & 4: *Uraba lugens* -- Spread ♂ & ♀; LFW. (length of forewing from base to tip, in a straight line) = 11 mm. (♂) & 14 mm. (♀) — (Blackwood, S. AUSTRALIA — April 1968 — uv. light). Figs. 2 & 3: Live ♂♂, in typical resting position; LFW. (both) = 11.5 mm. — (Blackwood — 1 Apr. 68 — uv. light).

The larvae are conspicuous on eucalypts around Blackwood from mid to late summer (Jan. through March), and again from mid winter to early spring (July through mid Oct.). Defoliation, when it occurs, seems to be associated primarily with the spring brood at Blackwood (Sep.-Oct.). They often seem to favor sapling eucalypts, or stunted and struggling smaller trees in poor condition. Incidentally, this apparent preference for unhealthy trees would appear to indicate their importance as "natural thinners". If, at times, they actually killed the weaker trees in a stand of eucalypts, the remaining nearby trees would thereby benefit from reduced competition.

PARASITES: Two species of small hymenopterous parasites, and one hyperparasite, were reared from a series of *U. lugens* larvae (N1.2A) collected on 28 Feb. 1977, along the west side of the Northwest Coastal Highway, about 6 mi. N. of Geraldton, Western Australia, on *Eucalyptus camaldulensis*. The nolid larvae were in about 2nd or 3rd instar when collected. The parasites killed their hosts in about 4th or 5th instar, and attached their cocoons to the foodplant leaves next to the shrivelled host remains. These parasites all emerged in March, 1977, and were code-numbered "H65", and "H67", the latter being the hyperparasite (4 of which emerged from one cocoon of "H65"); no determinations have been obtained for these wasps.

The other purpose of this paper is to draw attention to the fact that, in the Old World at least, this peculiar nolid larval habit of carrying about a stack of cast head capsules is by no means unique to only one genus or species, nor to Australia. In April 1971, while searching through the nolid drawers at the B.M.(N.H.), London, I came across specimens of two EUROPEAN nolids demonstrating precisely the same habit: *Roeselia togatulalis* Hubner (the first species appearing under *Roeselia* in the B.M. systematic collection), and *R. nitida* Hampson. The former was represented by many adult specimens from Germany, and four inflated larvae, one of which had a "cephalic horn" of four head capsules attached (main coll. and drawer 3-39, supplementary series). One of the dry larval specimens is attached to an unidentified, skeletonized leaf of what appears to be one of the deciduous, lobe-leafed oaks (*Quercus* sp.). In the main collection there is also a cocoon having the last instar cervical hair tuft (carrying two head capsules) attached to its outside at about middorsum, and projecting forward from its place of attachment just behind the highest point on the cocoon dorsum, which is at the upper (caudad) end of the emergence-slit. Under *R. nitida* one cocoon, similarly-decorated but with only one head capsule, was encountered (main collection).

Later, Mr. D. J. Carter, of the B.M. Ento. Dept. (in litt. — 1971-72) kindly provided me with a copy of some notes and sketches made in 1891 by "H. C. Harford, Major 2nd Wilt. Reg.", depicting this habit yet again in another nolid from INDIA. The moth involved was thought (by Harford) to be *Rhynchopalpus argentalis* Moore, but it appears that he was not entirely certain about the determination. Mr. Carter kindly took three color slides of the Harford sketches for me, and from these I was able to obtain two reasonably satisfactory black-and-white prints for inclusion in this paper (Figs. 11-12). The third, an excellent sketch of four larvae feeding on the foodplant leaves, was too pale for black-and-white reproduction. Handwritten notes jotted on the same page (around the three sketches) are interpreted as follows, some words being unclear: "1st spun up 14 May 91 — Out 11 June 91. Larvae sent to me by Major Gaje V Ghurkas(?) from Dharmsala. I also took one of the moths at Dalhousie, in my room. Food plant Ilex Oak. I gave the cocoon and one of the moths to the British Museum." (Mr. Carter has suggested the "Ilex Oak" might be *Quercus ilex* L..) Along the foodplant stem, in the larval sketch, was written the date "10-5-91", which should be interpreted as 10 May 1891 (not Oct. 5th).

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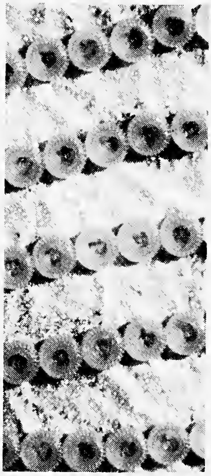

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Fig. 5 (left); *Uraba lugens* -- Unhatched living eggs; size = 0.50 X 0.25 mm. — (Blackwood — 1 Apr. 68); Fig. 5 (right): Empty (hatched) egg shells showing opercula ajar (S.E.M. photos). Fig. 6: Live final instar larva at rest on *Eud. odorata* leaf; length = 17 mm. — (Blackwood — 12 March 67); predominant dorsal groundcolor is pale-yellowish (cream ventrally), with hairs mostly whitish-cream.

Notes jotted beside the larval sketch were as follows: "As they appear when feeding.. As a rule they feed very close together. I have drawn them far apart on purpose. Underside of leaf — larvae feeding." Two of these larvae were drawn to show the dorsal surface; they have a profile fairly similar to that depicted in my Fig. 8, but with more pronounced segmentation. The maculation, however, is entirely different. There appears to be a thin middorsal black line, which enlarges into two black spots at the caudal end (A7-A8?), with a larger middorsal spot also on what appears to be A3, and a smaller subdorsal black dot on either side of what appears to be T3. The sketch is lightly watercolored, with the dorsal ground color depicted as pale yellow-cream, and a deeper golden-tan or very pale yellow-orange in the suranal region. The head capsules are shown as jet black, and the hair tufts joining the cast capsules are painted a rich medium-brown. Only two cast capsules are shown attached to each of the four larvae illustrated.

The date faintly written at the lower left of the stem, in the cocoon drawing (my Fig. 11), was interpreted as "23-5-91" (i.e. - May 23rd). Notes jotted beneath the sketch of cast head capsules (my Fig. 12) were quite clear, as follows: "A = Brown silken tuft springing out from behind the head; B = Head and skin of old shed skin."

The last example of head capsule retention by a nolid larva known to me, is from JAPAN. The nolid involved is *Memerastria mandschuriana* Oberthur. An adult, and a profusely-hairy larva carrying a cervical stack consisting of several attached head capsules, are both illustrated with good color photographs (Pl. 14, Fig. 35) by Mutuura et al. (1970). The species is also described in pp. 41-42, but I cannot comment further on this as the text is in Japanese. The scientific name of the foodplant is not given.

I have never seen this strange larval habit reported for any New World species, but it would certainly warrant watching for; particularly among the Mexican and Central or South American nolids whose life histories remain unknown.

Acknowledgements, Determinations, and Specimen Distributions: I would like to thank D. J. Carter of the Ento. Dept., B.M.(N.H.), London, for providing the xerox copy and slides of the nolid from India; also D. S. Fletcher, of the same Dept., for his help in sorting out the generic nomenclature associated with *lugens*; Dr. Allan Watson, David T. Goodger, and Maureen A. Lane (all of B.M., London), for providing the two S.E.M. photos used in Fig. 5; M. S. Moulds (Sydney, Aust.) for reviewing the manuscript in 1977 and offering constructive criticisms. Figs. 1-10, with the exception of the two S.E.M. photos in Fig. 5, are from photographs by the author; Figs. 11-12 are prints from color slides kindly provided by Mr. Carter.

All stages of the *U. lugens* life history from Black wood (plus notes) were deposited in the South Australian Museum (Ento. Dept.), Adelaide, under the McFarland code-number "N1.2", and some adults were given to B.M.(N.H.); Geraldton specimens, and associated parasites, were deposited in the Dept. of Agriculture (Ento. Section), South Perth, under "N1.2A".

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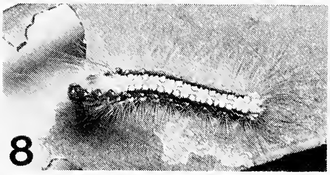

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Figs. 7-9: *Uraba lugens* -- Live final instar larvae (same data as for Fig. 6). Fig. 10: *Uraba lugens* -- Recently-formed cocoon with 3 attached head capsules; length = ± 22 mm. (Blackwood — late Mar. 67). Figs. 11 & 12: (?)*Rhynchopalpus argentalis*, cocoon and larval head caps., from sketches by H. C. Harford (Dharmsala, INDIA — May, 1891).

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The Depredations of the Large White Butterfly (*Pieris brassicae*) (Pieridae)

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Abstract.—An assessment is given of the damage caused by the Large White Butterfly. It is based on reports from the literature, from correspondence with entomologists in various countries, and from analysis of statistics of both the Ministry of Agriculture, Fisheries and Food (MAFF) and the Food and Agriculture Organization (FAO) of the United Nations. Eighteen economic crops are reported as food-plants of the Large White. Almost £1m ($1.85m)* of *brassica* crops would be lost annually in the United Kingdom with a 1% crop loss. In the Old World a loss of £110m ($204m) would be expected annually with a 4% crop loss, and in the New World £10m ($18.5m) could be the expected loss now that the Large White is established in Chile.

It seems appropriate that at a time when man is concerned with critically analysing his returns from crops, he should take a closer look at those insect species which cause small percentage losses over large crop areas. The aim of this paper is to assess the potential threat to Man's crops of the Large White.

Distribution of the pest: The Large White is found in 41 countries, principally in the Old World. It's distribution extends from the United Kingdom (UK) in the west to China in the east and northwards from the African coast to the Arctic Sea (Commonwealth Institute of Entomology 1976). In the last six years it has established itself successfully in Chile (Gonzalez 1972; Gardiner 1974), and now presents a problem in that country.

Devastations pre-1950: Descriptions of attacks on crops by the Large White were plentiful before the 1939-1945 war, when this insect was a more serious pest. Indeed, reports of migrations of "whites" as thick as snowstorms have been reported at intervals from 1556 (Nichols) to 1945 (Ford), including accounts of masses of wandering larvae (Guerne 1894) holding up public transport. From the reports in Europe before 1950 there are many cases of 100% loss of crop; in England, turnips (Cansdale 1876; Granville-Clutterbuck 1941), brussels sprouts (Theobald 1909), kale (Anderson 1909), cauliflower (Zanon 1919), kohl-rabi (Friederichs 1931). In Switzerland it was

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* Based on £1 = $1.85 at 18th Dec. 1977

TABLE I

Crops Recorded Eaten by P. brassicae
With An Indication of the Degree of Devastation

Common	Specific Name	Degree of Attack
Cruciferae		
Cabbage	*Brassica oleracea* var. *capitata*	1
Savoy	*Brassica oleracea* var. *capitata*	2
White	*Brassica oleracea* var. *capitata*	2
Blue	*Brassica oleracea* var. *capitata*	2
Red	*Brassica oleracea* var. *capitata*	2
Chinese cabbage	*Braccica oleracea* var. *capitata*	2
Brocolli	*Brassica oleracea* var. *capitata*	2
Rape swede	*Brassica oleracea* var. *gemmifera*	1
Brussels sprouts	*Brassica oleracea* var. *oleracea*	1
Cauliflower	*Brassica oleracea* var. *botrytis*	1
Kohl-rabi	*Brassica oleracea* var. *caulorapa*	1
Kale	*Brassica oleracea* var. *acephala*	2
Black Mustard	*Brassica nigra* (l.) Koch	2
Turnip	*Brassica rapa L.*	1
Radish	*Raphanus sativus L.*	2
Horse Radish	*Armoracia rusticana* Gaertn, Mey & Scherb.	2
Cress	*Lepidium* sp.	2
Watercress	*Rorippa nasturtium-aquaticum* (L.) Hayek	2

(Nonenclature after Clapham, Tutin and Warburg, 1962)

[1] Recorded in the literature as 'entirely eaten', 'defoliated',. . .

[2] Recorded as 'a foodplant' or as 'eaten'.

reported that both cruciferous and umbelliferous crops were destroyed by larvae at a density of 938 m^2 *(Pictet 1918).*

Devastations since 1950: The Large White is a serious pest in Central Europe and Central Asia; in the Netherlands it is regarded as an occasional pest which causes considerable damage, usually only in warm dry years (*e.g.* 1970) (van Driest, personal communication). In Sweden the Large White is a pest on all kinds of cabbage in the central and southern part of the country (Douwes, personal communication), and in Austria it is regarded as a serious pest on cabbage in five regions (near Linz, in Niedersterreich, Eisnastadt, Burgenland and near Graz) (Berger, personal communication), where it has been strictly controlled (Glaeser, 1974).

In Czechoslovakia all *brassica* vegetables are attacked by *P. brassicae* (Spitzer, personal communication) and in Rumania there have been serious attacks of cabbage crops in 1948-49, 1955-56, 1962-63 and 1970-71 (Mustata and Andriescu, 1973). In Poland, the second generation can also cause considerable damage to cabbage (Przybylski, 1968; Starega, personal communcication).

In India, rape and mustard seed have received attacks (Srivastava, 1970) and in Nepal the subspecies *Pieris brassicae nepalensis* has been responsible for considerable damage to cabbage (Chuang-Lung, 1976). *P. brassicae* can also cause serious damage to cabbage crops in Lebanon, Syria and Iraq (Talhouk, 1969); Turkey (Asena, 1974); and Russia (Jakimaricius, 1974).

In the UK, Belgium, France and China, the Large White is now regarded as an occasional minor pest (Depiveux, Milaire and Chaung-Lung, personal communications respectively).

Crops attacked: The larva of the Large White is oligophagous and is known from a wide variety of foodplants. It has been recorded from 114 foodplants in the wild, representing the families Cruciferae, Resedaceae, Papilionaceae, Umbelliferae, Tropaeolaceae (Feltwell, unpublished) and these include species and cultivars of economic crops.

The high risk-crops which are most susceptible to depredations ofthe Large White in Europe, are cabbages, cauliflowers, Brussels sprouts, rape, kohl-rabi, turnip and swede (Table 1). In the Middle East, capers are liable to attack.

Effect on the crop: It is often found that more damage occurs at the periphery of the crop than at the centre (Friederichs, 1931). Where complete defoliation occurs there is obviously no crop to market. Even slight damage can make the plant unsightly to the consumer and in particular larval frass spoils the market value of a crop.

Brassica production in the UK: The UK was expected to produce about 1m tonnes of cabbage, Brussels sprouts, cauliflower, turnips and swedes during 1976-77, with a market value of £99m ($183m) (Table II). During the same period, imports of cabbage, cauliflower and brocolli will amount to about £4m ($7.4m).

Ironically, in the UK no figures are available of the amount of brassicas grown in allotments, where often, because *P. brassicae* is uncontrolled, damage is severe. The number of allotments in the UK is rapidly decreasing. In 1945 there were 1.5m (Handiman Which, 1975), in September 1955 there were 1,004,656 (Best & Ward, 1956), in September 1973 'The Times' quoted 467,755 and in 1975 Handiman Which (*loc. cit.*) quoted about 333,000. Inspection of allotments today shows that brassicas are still grown on at least 5-10% of the total allotment area.

Information on the production of brassicas from gardens is also scant. Best & Ward (*loc. cit.*) stated that 374 kof cabbage, cauliflower and Brussels sprouts can be produced from a ten rod plot. They quoted £4.17.6d (£4.87½) as the value of the total yield of vegetables from each house with a garden in 1952, which would be equivalent to at least double that value today. According to Herwin (1977 pers. comm.) at least £0.75m ($1.39m) worth of crop is lost annually to the depradations of this pest in allotments and gardens.

Brassica production throughout the world range of P. brassicae: Data from the current FAO (1975) Production Yearbook shows that 18m tonnes of cabbage and cauliflower were produced in 1974 in Europe and Asia, and about 2m toones were produced in the Americas (Table III). World figures for the production of swedes and turnips in North and South America are not available.

Discussion: It is clear that the major areas of attack on brassica vegetables by the larvae of the Large White and its sub-species, are North and Central Europe, India, Nepal and China. It is likely that vegetables grown in the USSR and other iron curtain countries also currently suffer devastations from the Large White but information from these sources is not forthcoming. Some concern over the spread of the Large White in South America, and thus to the rest of the Americas, is felt with its successful establishment in Chile in 1972. In the UK the Large White is now less of a problam that it was before 1955 when an epizootic virus naturally disseminated the resident population (Smith, 1956). Added to this, British farmers regularly use DDT and organophosphorus insecticides, such as mevinphos and trichlophon, to kill cabbage caterpillars.

In order to assess on a world-wide scale, the damage caused by the Large White and its sub-species, it is necessary to take into consideration the following factors:

(i) attacks are often extremely localized and in small areas crop loss can be 100%

(ii) the strongly migratory habit of the Large White helps to disperse it over wide areas and may help it to infest areas previously free from attack.

(iii) the larvae can develop on a wide variety of foodplants, including both cultivated and wild crucifers.

(iv) populations are regulated by a large number of predators, hymenopterous parasites and micro-organisms such as viruses, bacteria, protozoa and fungi.

(v) warm and dry years usually result in an increase in the population of this insect.

The above factors make an assessment of the overall degree of attack by this pest extremely difficult. Furthermore, there are communication difficulties in obtaining first-hand information about the degree to which *P. brassicae* attacks crops in the various countries within the world range and indeed about each species of crop attacked. However, taking the four brassicas most attacked in the UK as an example (Table II), a 1% loss due to the Large White would result in a loss of approximately £1m ($1.85m) worth of crop in 1977. In countries such as Austria, Poland and Sweden where damage is more severe, many millions of pounds worth of crop must be lost to *P. brassicae.*

Europe and USSR produced 11m tonnes of cabbage and cauliflower in 1974 (Table III). If a 4% theoretical loss of yield is applied for this region, the tonnage lost would be about 0.35 tonnes or about £35m ($55m) based on 1977 prices. (Forecast average of the two is nearly £100 ($185) tonne. In Asia and China, the production of cabbages for 1974 was about half that of Europe and for North and South America about one third. Thus one could tentatively calculate that at least £60m ($111m) worth of cabbage and cauliflowers are lost annually in Europe and Asia. Bearing in mind that this figure has not been corrected for inflation and also does not include either the other 18

TABLE II

Production of Value of the Four Principal Foodplants of Pieris brassicae in the United Kingdom

Crop **Hectares**

Crop	**Hectares**	**Tonnes**	**Value of output (£)**	**($)**
Cabbage	**24,581**	**468,900**	40,810,000	75,498,500
Imported	—	14,800*	1,646,000*	3,045,100
Brussels sprouts	13,351	141,700*	25,506,000	47,186,100
Cauliflower	14,340	193,100	21,394,000	39,578,890
Imported (+brocolli)	—	16,500*	2,018,000*	3,733,300
Imported (+Channel Isles)	—	6,000*	638,000*	1,180,300
Turnips and swede	5,239	124,000	7,428,000	13,741,800
Totals	**57,511**	**975,000**	**99,440,000**	**184,014,000**

(based on Ministry of Agriculture, Fisheries and Food Statistics 1976/77 Forecast.)

* only figures available 1975/76

TABLE III

Cabbage and Cauliflower Production in Europe,, USSR and Asia, 1974

Country	Tonnes of cabbage	Tonnes of cauliflower
Europe	7,698,000	2,128,000
Asia and China	3,959,000	851,000
N. America	1,504,000	151,000
S. America	180,000	60,000
Europe USSR	3,218,000	298,000
Total	**16,550,000**	**3,428,000**

(based on FAO (1975) Production Yearbook for 1974) species of crop attacked or the crops attacked in non-commercial areas, gardens and allotments, the figure for destruction to all crops could easily to nearer to £100m ($185m). A potential threat of about £10m ($18.5m) loss per annum in the Americas is posed by the presence of *P. brassicae.*

It is therefore clear that a considerable amount of potential human food is eaten each year by the larvae of *P. brassicae*; and that the major areas of infestation are Central Europe and Asia. The possibility of returning £110m ($204m) worth of food material to Man each year, is an incentive to look for an effective way of control of the insect; even a 50% reduction in the world population of *P. brassicae* would return £30-50m ($56-93m) worth of crops to hungry mouths in both developed and underdeveloped countries.

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Notes on the first-instar and two parasites of the Clover cutworm, *Scotogramma trifolii* (Noctuidae; Hadeninae)

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Abstract. — The first-instar larva of the Clover cutworm, *Scotogramma trifolii* (Noctuidae; Hadeninae), is described. Additionally, *Euplectrus* sp. (Hymenoptera; Eulophidae), an ectoparasite, and *Spoggasia tachinomoides* (Tns.) (Diptera; Tachinidae), an endoparasite, are reported for the first time from *S. trifolii*.

Introduction

Larvae of *Scotogramma trifolii* (Hufn.) are polyphagous and feed normally on plants of the family Chenopodiaceae. While this noctuid species does not usually cause economically significant losses, damage occasionally results from its feeding on a variety of crop plants including clover, alfalfa, cotton, sugar beets, and tomatoes (Cayrol, 1972). In the autumn of 1976, an epizootic caused by a granulosis virus decimated a large larval population of *S. trifolii* feeding on Russian thistle, *Salsola iberica* (Sennen and Pau), in southern California (Federici, 1978). To aid in experiments on interactions of this virus with its host, a colony of *S. trifolii* was established from field collected larvae and a semi-defined larval diet was developed (Santiago-Alvarez *et al.*, 1979). The establishment of this colony allowed us to study the immature stages of *S. trifolii.* Although larvae of this species have been described previously, most descriptions concern late instars (Beck, 1960; Crumb, 1956; Godfrey, 1972; Tkho, 1972), with little attention to the first-instar except for the study of Soures (1948). In this paper the first-instar is described. Additionally, observations are reported on two larval parasites obtained from field collected larvae, and a method for determining pupal sex is given.

Observations

First-instar larva: The first-instar larva is cylindrical in shape, approximately 2 mm in length, light grey in color and translucent (Fig. 1). The head is wider than the first thoracic segment and light brown in color. There are dark brown papillae distributed over the cranial cuticle, more densely concentrated in the genal regions and forming a V on the epicranium. There are six stemmata, four in the lateral position forming a semi-circle and two more ventrally. The dorsal shield is not distinct.

The body dorsum is covered with numerous black setae which arise from black papillae. In the thoracic segments these setae are aligned in a transverse row and distributed evenly across the segment posteriorly. In the abdominal segments the setae are distributed in two alternating rows. A similar pattern of setal arrangement has been noted in *S. defessa* by Comstock (1966).

Fig. 1. The first-instar larva of *Scotogramma trifolii* (Hufn.) X20.

There are five pairs of prolegs, each with crochets. The prolegs are located on the third, fourth, fifth and sixth abdominal segments in addition to the anal segment. However, the prolegs on the third and fourth abdominal segments are smaller and not as well developed as those on the fifth and sixth abdominal segments. The first and second instars of *S. trifolii* resemble larvae of the subfamily Plusiinae in appearance yet walk more like geometrid larvae. The prolegs on the third and fourth abdominal segments apparently aid in this type of walking behavior. The presence of prolegs on the third and fourth abdominal segments is an interesting observation because these prolegs were not observed in the first instar larva of *S. defessa* (Comstock, 1966) or *S. trifolii* in North Africa (Soures, 1948).

Except for species in which the last instar larvae lack the first two pairs of prolegs (i.e. Plusiinae), first instar larvae show no evidence of prolegs on the third and fourth abdominal segments (Ripley, 1924). However, among other subfamilies of Noctuidae the reduction or absence of the first pair, or both the first and second pair of prolegs in first- instar larvae, is a condition found commonly in many species throughout the Agrotinae, Hadeninae, and Acronyctinae (Beck, 1960). Apparently, the evolutionary development of the reduction or absence of the prolegs among species in these subfamilies has originated independently.

The differences observed in the first instar larva of *S. trifolii* as described here and that reported from North Africa (Soures, 1948) may be due to different selection pressures on the two widely separated populations, and further may indicate these populations represent subspecies.

The other instars of *S. trifolii* examined during the present study were identical to those described by Beck (1960) both in appearance and cheatotaxi.

The pupa and sex determination: Newly formed pupae are light brown under reflected light but gradually darken during metamorphosis becoming almost black just before eclosion.

Once the pupal cuticle is tanned, the morphological features required to determine sex are obvious. These features are illustrated in Fig. 2.

Natural parasites: Among sixty late instar larvae collected from a field of Russian thistle near Valley Road, Fontana, California, on June 4, 1977, eight were parasitized by two different parasites. On three of these larvae from 7 to 9 larvae of an ectoparasite, *Euplectrus* sp. (Hymenoptera; Eulophidae), were found between the last thoracic and first abdominal segment in the dorsal position. This parasite is a new species and its description is in progress (Gordh, G., personal communication). During the early stages of parasitization, the host larva fed and moved about normally on thistle plants maintained in the laboratory. However, after the parasites completed larval development, they moved to the ventral side of the host larva. Eventually, they made cocoons with an extensive silk mesh. This mesh immobilized the host larva and resulted in its death.

The other five larvae of *S. trifolii* were parasitized by an endoparasite, *Spoggosia tachinomoides* (Tns.) (Diptera; Tachinidae). Three of these larvae died before pupation and from each of these a single parasite larva emerged and pupated. The remaining two host larvae pupated, and the parasite larva emerged and pupated after leaving the host pupa. Of the five parasite pupae obtained only one adult emerged. This adult was used for identification.

Thompson (1944) did not mention these parasites in *S. trifolii* and to our knowledge this is the first record of them from this species.

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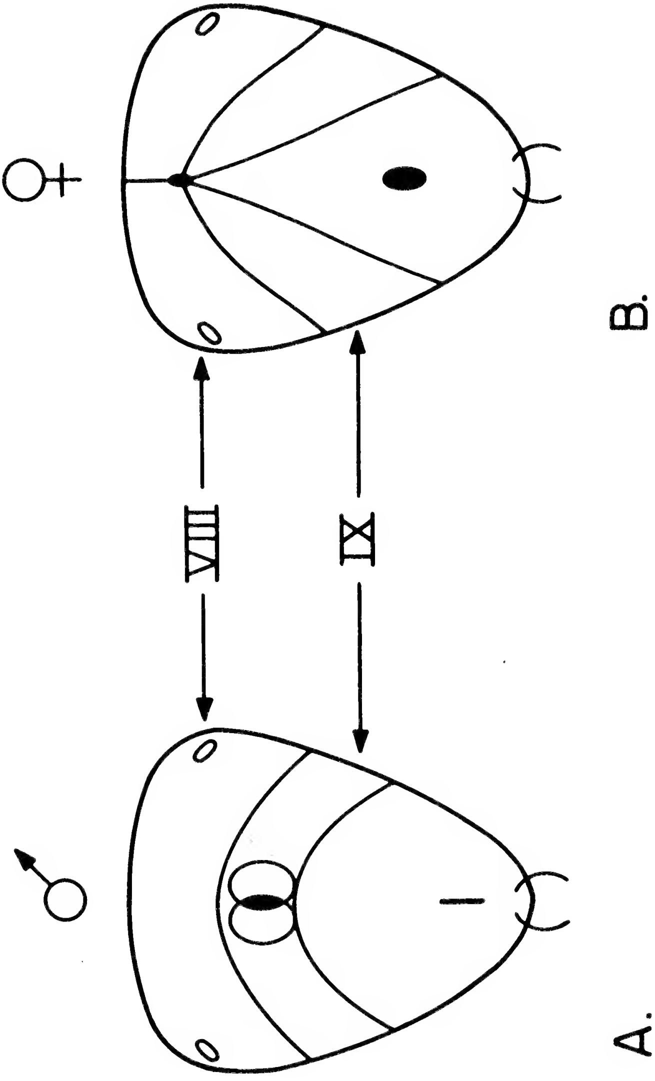

Fig. 2. Ventral terminal abdominal segments of male and female pupae of *Scotogramma trifolii.*

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Similarities and differences in forewing shape of six California Catocala species (Noctuidae)

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Abstract.—The results of a biometrical study of the forewing sizes and proportions of six California species and subspecies of small yellow-winged *Catocala* are presented. Three hundred eighty-four specimens were used. Means of the wing margin lengths and of the ratios of the lengths of the costal, outer and inner margins are compared. The ratios are used to calculate a proportionality product for each of the taxa. The data indicate that the six entities are distinct taxa. On the bases of wing shape and proportion, they can be divided into three distinct groups, supporting previous judgments of similarities between some of the taxa, and placing recently described species in relation to the rest.

Introduction

In California are found six species and, or, subspecies of small yellow-winged Catocalas. They are *Catocala chelidonia* Grote (1881), *Catocala andromache* Henry Edwards (1885), *Catocala mcdunnoughi* Brower (1937), *Catocala andromache* subspecies *benjamini* Brower (1937), *Catocala californiensis* Brower (1976), and *Catocala johnsoniara* Brower (1976). The adults of these taxa resemble each other closely in size, general coloration, and appearance. Barnes and McDunnough (1918) grouped the species then known together. This was done also in the McDunnough checklist (1938). Of interest to the biologist are the relationships of the taxa and the origins of the group. Are they species of diverse origins that have become similar through convergent evolution? If the group is of monophyletic stock, new problems of evolution and speciation arise. The authors have taken as many as four of the six taxa in the same locality in the same night, specifically *andromache andromache, andromache benjamini, californiensis,* and *chelidonia.* At another locality *andromache andromache* and *johnsoniana* are taken together. If the group is monophyletic, what evolutionary mechanisms have facilitated the diversification of the species and maintained the genetic isolation of these sympatric taxa? These questions, in fact, are of central importance to an understanding of the evolution and speciation of the Genus *Catocala* as a whole (Sargent 1976 p. 77 ff.) The six taxa are illustrated in Figure 1.

While the earliest-described species have been known for nearly a century, little has been published about their food plants and immature stages (Barnes and McDunnough 1918 p. 33, Brower 1976 p. 33). With only the adult stages available for comparison little progress has been made toward clarifying their phylogenetic history and relationships. Brower (1937 p. 784) in the species descriptions of *mcdunnoughi* and *benjamini* calls attention to a resemblance between *mcdunnoughi* and *chelidonia,* and assigns *benjamini* to the status of a subspecies under *andromache.* No further comparative studies have been made since.

Beginning about 1930 the authors have collected, observed, and studied the taxa in captivity and in the field. These efforts have yielded significant data on the distributions, flight periods, immature stages, food plants, and aspects of the adult structure other than wing colorations and patterns. From the knowledge that has been gained fresh insights into the relationships of the six taxa soon may be afforded. Reports on our studies of these matters are forthcoming. The present paper describes the results of a study undertaken to seek evidence of the relationships of the taxa by use of structural characteristics other than pattern and color. Using biometrical methods the authors chose, specifically, the size, shape, and proportions of the forewings for a comparative study of the six members of the group.

Procedure

Three hundred eighty-four specimens were used, all field-caught over periods of years, and constituting random sets selected only to the extent of discarding specimens with wings too damaged to allow accurate measurement. Three dimensions were measured on the front wing. The first was the length of the costal margin from the wing base to the distal end of vein Radius 2. The second dimension was the length of the outer margin from the end of vein Radius 2 to the distal end of the 2nd anal vein. The third dimension was the length of the inner margin from the end of the 2nd anal vein to the wing base. The measurements were made on dried, spread specimens under magnification with a set of dividers and read to the nearest half millimeter. The right wing was measured unless damaged required measurement of the left.

Results

Size

In determining the size means of the wing margins for each of the six taxa the means for the two sexes were first obtained and then averaged for the species mean. This was done because one sex, usually the female, was represented in the sample more often than the other.The females tend to be larger in all of the taxa. This would have skewed the species means if the measurements of both sexes had been lumped together. The means of the six taxa may be compared in Table 1.

The means show a progression in size from *chelidonia,* the smallest species, to *johnsoniana,* the largest. While *johnsoniana* and *andromache andromache* fly together in central California, and *chelidonia, californiensis, andromache andromache,* and *andromache benjamini* may be taken in one locality in southern California, yet the population of each taxon has a characteristic mean size of the forewings distinct from that of the others with which it may be associated. These differences in size clearly indicate that none of the recognized taxa are polymorphisms of a lesser number of species.

TABLE I
MEANS OF FOREWING MARGIN MEASUREMENTS

Species Name	Sex	Sample Size	Mean Lengths			Three Margin Sum
			Costal Margin	Outer Margin	Inner Margin	
Catocala	M	9	19.2mm	11.8mm	15.6mm	
chelidonia	F	41	19.7mm	12.1mm	16.1mm	
	Species	50	19.5mm	12.0mm	15.9mm	47.4mm
Catocala	*M*	*38*	*19.4mm*	*11.8mm*	*15.1mm*	
a. benjamini	F	52	21.1mm	12.7mm	16.2mm	
	Species	90	20.3mm	12.3mm	15.7mm	48.3mm
Catocala	M	16	20.2mm	12.1mm	15.3mm	
californiensis	F	50	21.3mm	12.9mm	16.5mm	
	Species	66	20,8mm	12.5mm	15.9mm	49.2mm
Catocala	M	39	20.5mm	12.5mm	15.9mm	
a. andromache	F	46	21.2mm	12.9mm	16.5mm	
	Species	85	20.9mm	12.7mm	16.2mm	49.8mm
Catocala	M	36	20.3mm	12.4mm	16.0mm	
mcdunnoughi	F	28	21.9mm	13.5mm	17.4mm	
	Species	64	21.1mm	13.0mm	16.7mm	50.8mm
Catocala	M	16	21.5mm	12.3mm	16.6mm	
johnsoniana	F	13	22.5mm	12.7mm	17.3mm	
	Species	29	22.0mm	12.5mm	17.0mm	51.5mm

Wing Shape

To compare the differences in wing shape and proportions of the six taxa two types of data were used. The first was the means of the linear measurements of the wing margins given in Table 1. Comparing *chelidonia* with *benjamini,* while the costal and outer margins of *chelidonia* are shorter than those of the larger *benjamini,* the length of the inner margin of *chelidonia* exceeds that of *benjamini.* Thus the *chelidonia* forewing, by having a longer inner margin, must have an outer margin that is less oblique, altering the size of the apical and outer angles and making the wing more blunt. A close inspection of the wings of the two species confirms that the forewings of *chelidonia* are relatively broader and more blunt than the forewings of *benjamini.*

Comparing the mean length of the outer margin of *johnsoniana,* the largest species, with those of *mcdunnoughi, andromache andromache,* and *californiensis,* it is found that the outer margin mean length of *johnsoniana* is less than that of *mcdunnoughi* and *andromache andromache,* and equal to *californiensis.* The short outer margin of *johnsoniana* indicates the forewing to be relatively and actually narrower than those of the other three species. Again this is confirmed by examination of the specimens. As size differences between the species become limiting, the use of the linear measurements directly for further comparisons of the wing proportions of the species cannot be continued.

Wing Proportions

From species to species as wing shapes, angles, and proportions change, one would expect the wing margin lengths to change in correlated fashion. Accordingly, to eliminate the limitations on comparisons of wing shapes and proportions imposed by size differences, the original data, consisting of the linear measurements of the wing margins, were converted into ratios. Such ratios derived from the margin lengths should be similar for wings of the same shape and proportions. Two ratios were used: the first, the ratio of the costal margin length to the outer margin length; the second, the ratio of the costal margin length to the inner margin length. The ratios were converted into decimal values for each of the specimens used in the study and the species means determined. Finally, the species means of the two ratios were multiplied to yield a product of proportionality for each species. Thus a single value was obtained characterizing the forewing proportions of each species. It was found to be unnecessary to keep the data separate for the two sexes, as the ratios for both sexes of a species were quite the same. The proportionality data are presented in Table 2. The data are graphed in Figure 2.

Broad blunt wings should have comparatively long outer and inner margins. These, when divided into the costal margin lengths, should give low proportionality ratios. A comparison of *chelidonia* and *mcdunnoughi* with the other taxa discloses that ratios and products for both are lower than those of the rest. The differences in their products from the others are significant (P is less than .0001 for both.). The data confirm the resemblance between these two species first observed by Brower. The difference between *chelidonia* and *mcdunnoughi* is significant also (P equals .012).

Narrow wings with more oblique outer margins may be expected to have shorter outer and inner margins that yield larger ratios and products. We find that the ratios and products of the remaining four taxa are larger and representative of such wing shapes and proportions.

The proportionality ratios and products of *andromache andromache, andromache benjamini,* and *californiensis* have similar values, setting these three taxa apart as a middle group of species. The products of the three differ significantly from those of *chelidonia, mcdunnoughi,* and *johnsoniana* (P is less than .001 for all.). Among the three the product of *californiensis* differs significantly from both *andromache benjamini* and *andromache andromache* (P equals .007 and less than .001 respectively.). This confirms the distinctness of *californiensis* as a species from the other two. The difference between *andromache benjamini* and *andromache andromache* is not significant, supporting Bower's judgment in treating these two taxa as subspecies of a common species.

The costal margin-inner margin ratio of *johnsoniana* is equal to those of *andromache benjamini* and *andromache andromache.* But the costal margin-outer margin ratio and proportionality product of *johnsoniana* are the highest of the group and distant from the rest. These differences are highly significant.

TABLE II
FOREWING MARGIN PROPORTIONALITY RATIOS AND PRODUCTS

	Costal-Outer Margin		Costal-Inner Margin		Ratio Products	
Species	**Ratio Mean**	**Standard Error**	**Ratio Mean**	**Standard Error**	**Prod. Mean**	**Standard Error**
Catocala chelidonia	1.63	.0079	1.23	.0044	2.00	.012
Catocala a. benjamini	1.65	.0058	1.29	.0037	2.13	.0096
Catocala californiensis	1.66	.0066	1.31	.0045	2.17	.011
Catocala a. andromache	1.64	.0057	1.29	.0034	2.11	.0093
Catocala mcdunnoughi	1.62	.0066	1.26	.0040	2.04	.010
Catocala johnsoniana	1.76	.011	1.29	.0051	2.27	.017

Summary

Until sufficient material is available for a comparative study of the immature stages, generalizations about the relationships and phylogeny of the six taxa should not be attempted. However, this comparative analysis of the forewing sizes, shapes, and proportions indicates:

1. The distinctness of the populations of the six taxa, each having a characteristic mean size;
2. Measureable differences in wing proportions exist that can be characterized by numerical ratios and products useful for comparisons;
3. A group of two species, *chelidonia* and *mcdunnoughi,* with relatively blunt, broad wings;
4. A group of three taxa with moderately narrow and acute wings, *andromache andromache, andromache benjamini,* and *californiensis;*
5. A statistically significant difference between *californiensis* and the two *andromache* subspecies.
6. A close resemblance between the two *andromache* subspecies, the difference not being statistically significant;
7. A third group of one species, *johnsoniana,* with very narrow wings in proportion to their length, and the largest of the six taxa in size.

Acknowledgments: The authors express their thanks to Mr. Gordon Marsh, Museum of Systematic Biology, University of California, Irvine, to Dr. Charles L. Hogue and Mr. Julian P. Donahue and their staffs, Department of Entomology, Los Angeles County Museum of Natural History, for their assistance in securing needed publications, to Dr. A. E. Brower for identification of specimens, to Mr. and Mrs. Hugo Kinner for collecting privileges on their property, and to Mr. Ronald Leuschner for information on species distributions.

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Editors Note: One of the reviewers and myself were concerned with the matter of reference to the sympatric occurence of two subspecies, i.e., *andromache* and *benjamini.* The reviewer's comments were:

"If *andromache* and *benjamini* are subspecies, how could you have collected them in the same place? *Benjamini* is supposed to be an Arizona subspecies and should not occur within the range of nominate *andromache,* unless you were in some sort of blend or overlap zone. In general, if two things occur together and remain consistently distinct, they are species, not subspecies."

"A further comment on the subspecies problem. I do not understand how you could expect significant differences between samples of two "subspecies" collected in the same place. They should all be the same subspecies in southern California, unless *benjamini* is really just a color form that can occur anywhere. Its status may need to be reexamined."

Mr. Johnson answered these questions as follows, thus clariflying the matter:

"While *andromache andromache* is primarily a species of the coastal slopes of the Sierras and mountains of southern California, and *andromache benjamini* is a taxon of the desert slopes and Arizona, their ranges overlap and they have sympatry at points along the desert slopes of the high ranges of southern California. When Brower described *benjamini* from Arizona material, it was not known that *benjamini* populations existed in California also. I have sent a letter to Brower on Tuesday, October 23, 1979 calling his attention to the fact that in the zone of overlap there are no intergrades or hybrids, and that I have succeeded in rearing both species from ova to adult, finding that the ova and larvae are quite different. (These data being readied for publication now). In courtesy to Dr. Brower, who is preparing the *Catocala* volume for *Moths of North America,* I have left this designation of *benjamini* as a full species to him. In the present paper the wing proportion data of themselves do not support a change of *benjamini* to a full species, I have purposely avoided the change."

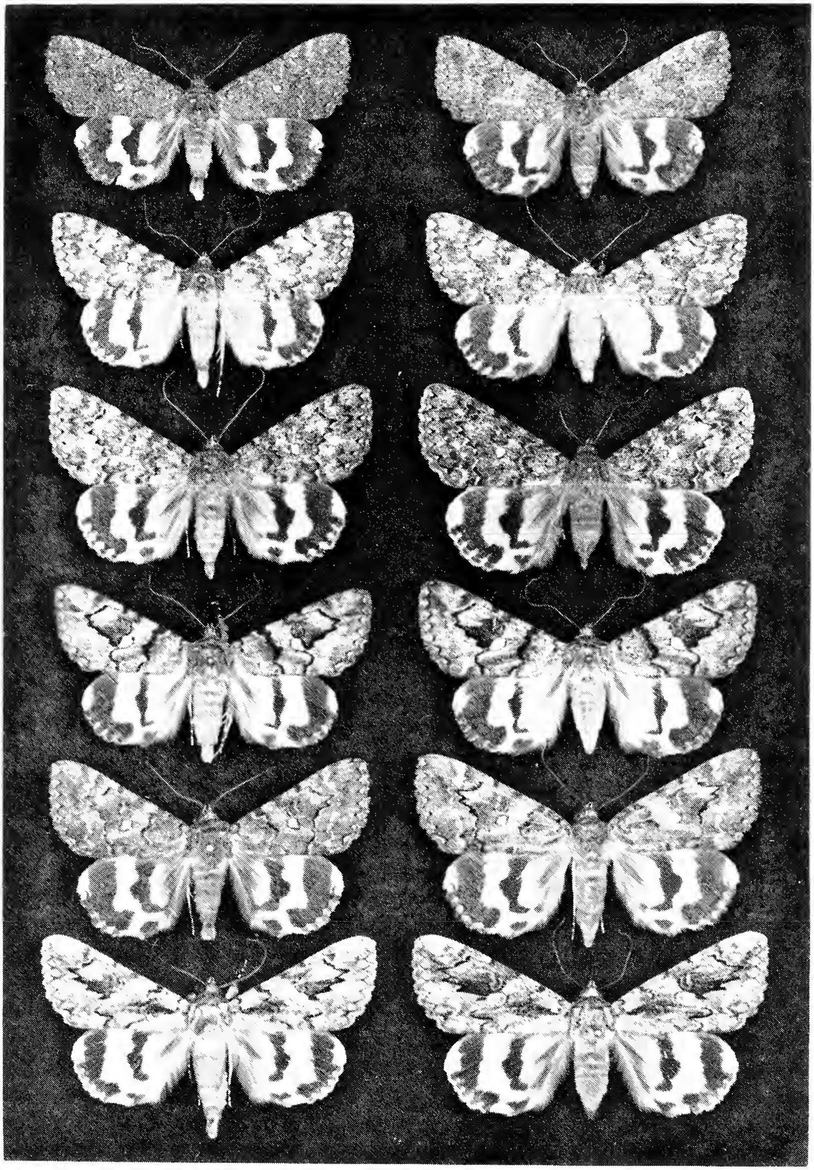

Figure 1. Pairs, male left, female right, from top downward, of: *Catocala chelidonia, Catocala andromache* subspecies *benjamini, Catocala andromache* subspecies *andromache, Catocala californiensis, Catocala mcdunnoughi,* and *Catocala johnsoniana.*

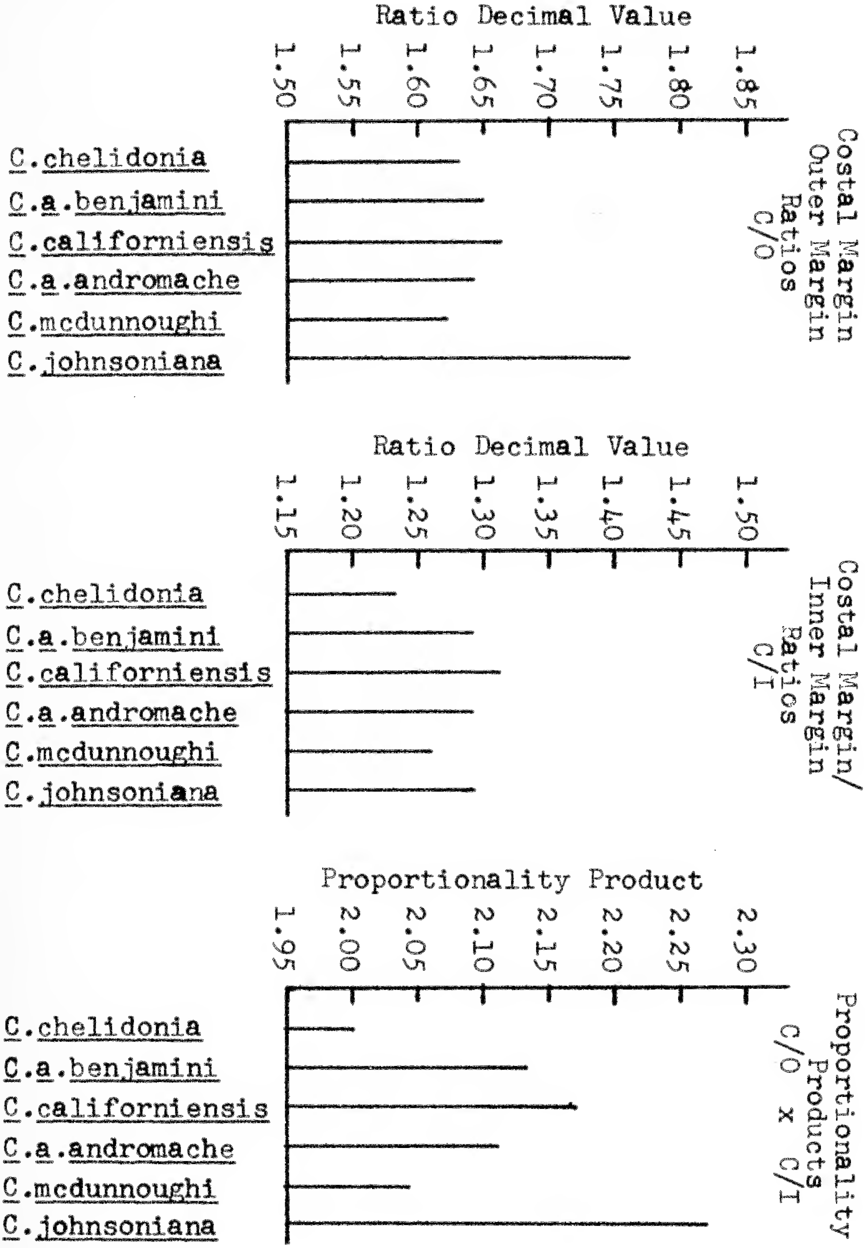

Figure 2. Graphs of Forewing Margin Ratio Decimal Values and Proportionality

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Asynaptic Meiosis in three species of Lepidopteran males

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Abstract.—Studies on the spermatocytic chromosomes from late pupal preparations of three lepidopteran species, *Arctia ricini* Fabr., *Polytela gloriosae* Fabr. and *Precis lemonias* Linn. have revealed a very low frequency of anomalous diakinesis and metaphase I cells. Many unpaired bivalents were observed having parallel oriented homologues, well separated from each other, in addition to some normal bivalents. Such early resolution of many bivalents to univalent homologues might have been either due to lack of chiasmata or due to presence of weak chiasmata undergoing rapid terminalisation. Since this feature appeared as early as late diplotene and diakinesis, the lack of chiasma formation still earlier in pachytene might have given rise to asynaptic meiotic patterns leading to anaphasic irregularities resulting in abortive seggregation of homologues. Since asynaptic meiosis is observed in late pupae, hormonal factors as well as genetic factors might be responsible for initiating the process.

The occurrence of achiasmatic meiosis has been reported in many animal species (Bauer 1953; White 1954; Ullerich 1961; Suomalainen 1965; Suomalainen et al. 1973). It is best known in certain groups of insects where the heterogametic sex usually shows asynaptic meiosis during gametogenesis (Beermann 1954; White 1954, 1973). The Lepidoptera, which exhibit female heterogamety, have not been considered to have chiasmata formed in females during oogenesis. Distinct chiasmata do occur during spermatogenesis in males (Maeda 1939; Federley 1943, 1945; Suomalainen 1965, 1969; Suomalainen et al. 1973; Traut 1977). Exceptional asynaptic chromosomes have been reported from abnormal spermatocytes in meiotic male lines by Srivastaa and Gupta (1962) in *Philosamia ricini* and by Virkki (1963) in *Diatrea saccharalis.* In this connection studies made on the spermatocytic chromosomes of three lepidopteran species, *Arctia ricini* Fabr. (Arctidae), *Polytela gloriosae* Fabr. (Noctuidae) and *Precis lemonias* Linn. (Nymphalidae) have revealed similar anomalous features during the first meiotic prophase which are reported below.

The larvae of *Arctia ricini, Polytela gloriosae* and *Precis lemonias* were collected from their respective host plants and were reared in the laboratory. Testes of mature larvae and pupae were dissected and were fixed in 1:3 acetic acid-ethanol. Permanent squash preparations of the materials were made and the slides were stained, in Heidenhein's iron haematoxylin. The chromosomes were drawn using a camera lucida with a total magnification of about Ca x 2000.

Gonial metaphases in *A. richini, P. gloriosae* and *P. lemonias* revealed 62 minute, almost equal sized dot shaped chromosomes showing the diploid chromosome number, 2n=62 in all the three species (Fig. 1, 4 & 7). Normally in all diakinesis and metaphase I plates 31 bivalents were encountered and the kiakinetic bivalents showed chiasma bearing shapes live 'V' rod, dumb-bell- and cross-shaped structures. The first metaphase bivalents were maximum condensed and appeared oval (Fig. 2, 5 & 8). However, a very low percentage of abnormal primary spermatocytes of pupal testes revealed a large number of univalent chroosomes in addition to some bivalents during diakinesis and metaphase I of all the three species (Fig. 3, 6 & 9. In the diakinetic cell of *A. ricini* (Fig. 3) 18 bivalents and 26 nonpaired univalents; in metaphase I of *P. gloriosae* (Fig. 6) 12 bivalents and 38 univalents and in *P. lemonias* (Fig. 9) 22 bivalents and 18 univalents were observed The disposition of the univalent chromosomes in closely associated pairs, without any contact, indicated these may be the unpaired homologues of bivalents which have either failed to form chiasmata or which had undergone early terminalisation, while in normal cells (Fig. 2, 5 & 8) pairing continued until first metaphase of all bivalents. Since, these features appeared as early as diakinesis involving majority of bivalents and terminalisation in normal cells is not complete until first metaphase they might have arisen through nonpairing of homologues even early in diplotene and not through early resolution. Although the number of cells involved were less, yet it was not insignificant. Since, their frequency increased from early pupa to eclosion with an increase in the involvement of bivalents until all bivalents showed unpaired homologues. Each of the secondary spermatocytes showed 31 univalent chromosomes at metaphase II without exception indicating a normal segregation of homologues in the second anaphase.

Normally meiosis is achiasmatic in the females and chiasmatic in the males of Lepidoptera (Maeda 1939; Federley 1945; Suomalainen 1965; Suomalainen, Cook and Turner 1977), although genetic data showing crossing over between a pair of linked genes in *Ephestia kuhniella* females suggest indirect evidence of chiasma formation (Kuhn and Berg 1855). Further Virrki (1963) has observed both chiasmate and achiasmate meiotic cells in variable proportion in the male pupae of *Diatrea saccharalis.* The findings of the present work is

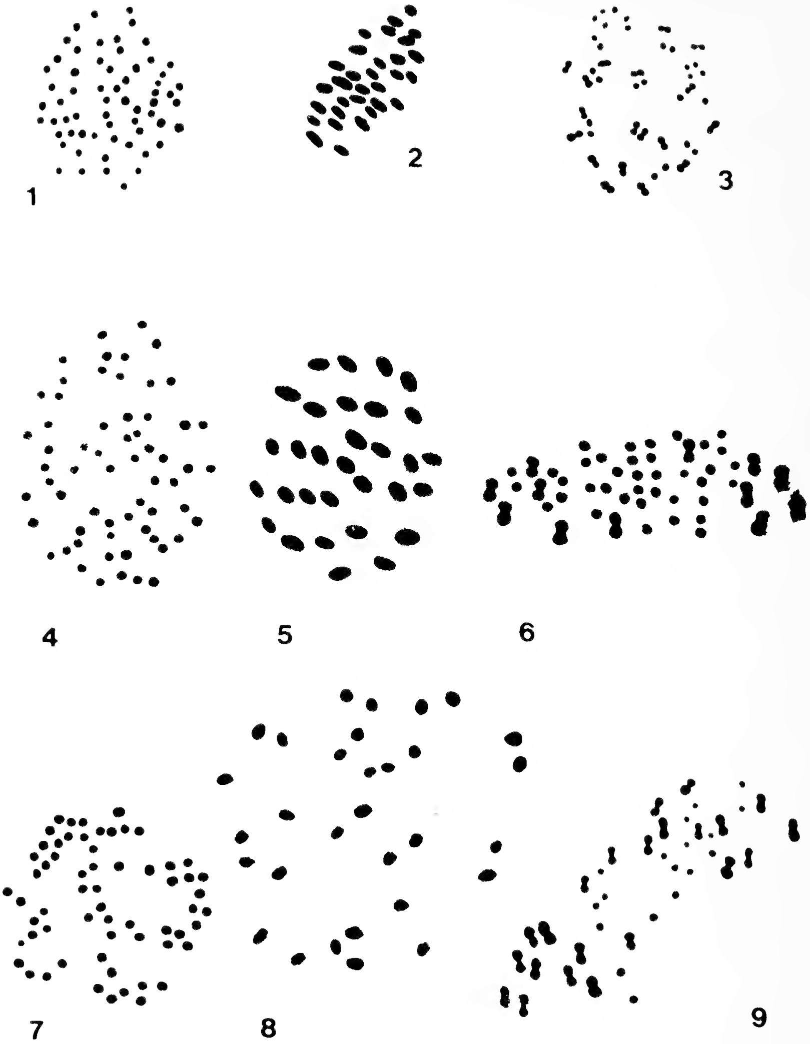

Fig. 1 to 3 Meiotic chromosomes of *A. ricini.* x2000 (Approx.). Fig. 1 gonial metaphase Fig. 2 metaphase I Fig. 3 abnormal diakinesis showing 18 bivalents and 26 univalents. Fig. 4 to 6 Meiotic chromosomes of *P. gloriosae.* Fig. 4 gonial metaphase Fig. 5 metaphase I Fig. 6 abnormal metaphase I showing 12 bivalents and 38 univalents. Fig. 7 to 9 Meiotic chromosomes of *P. lemonias.* Fig. 7 gonial metaphase Fig. 8 metaphase I. Fig. 9 abnormal metaphase I showing 22 bivalents and 18 univalents.

almost in close correspondence with that of Srivastava and Gupta (1962) and Virrki (1963). In all the three species viz. *Z. ricini, P. gloriosae* and *P. lemonias* normal diakinesis and first metaphase nuclei showed 31 bivalents. The diakinetic bivalents showed chiasma configurations.Exceptionally, a low frequency of cells showed many univalent chromosomes along with few bivalents at metaphase I. The univalent chromosomes lie in closely associated but quite separated pairs and are the homologues of corresponding bivalents of normal cells. The univalents result either from precocious terminalisation of chiasmata or have been formed without homolog pairing in meiotic prophase. The latter appears more probable. If there had been precocious terminalisation of chiasmata, so many chromosomes would not have been involved early in diakinesis, when in corresponding normal cells all the chromosomes have chiasmata continued up to metaphase I. Again in that case the univalents would indicate splits into chomatids, which they did not do. Such independence of the chromatids would lead to post reductional meiosis as in females while prereductional meiosis occurs in the males. In the vast majority of cases the chromosomes enter metaphase as single bodies. Since unpaired chromosomes appear at early diakinesis their resolution might have occured still earlier in a diplotenic split between homologues. The frequency of such cells showing asynaptic meiosis, though infrequency, is not insignificant. Furthermore, their number increases from early pupa to late pupa where all the chromosomes of such cells show the feature. This corresponds with similar observations made by Virrki (1963) in *D. saccharalis.* Anomalous pairing was also reported by Federley (1943) in *Dieranura* hybrids where the homologous chromosomes did not pair. However, there is no indication of hybridism here, since the phenomenon does not involve all cells. Although asynaptic segregation of homologues usually leads to anaphasic irregularities producing abnormal spermatozoa that perish, normal segregation also occurs, since at metaphase II invariabley 31 chromosomes have been scored in all cells.

The exact cause of such a synaptic formations are speculative. Beadle (1933) holds a single gene to be responsible for such anomaly in dysynaptic maize. Virrki (1963) has considered chromosome events to have influence on asynapsis in *Diatrea* where the asynaptic chromosomes appeared undercondensed in premetaphase and metaphase of first divisin. In his opinion genes and environment are not the only factors controlling asynapsis which appears only at a certain developmental phase. He presumes some other development control factors to be involved. Studies on the development of insects have revealed that larval ontogenesis and continuation of gametogenesis are under the control of the juvenile hormone (HR) secreted by the corpora allata. Before pupation this hormone ceases. The ineffectiveness of this hormone causes abortive trends in meiosis during pupal stages while the prothoracic hormone, acdysone, maintains normal spermatogenesis. Consequently it may be concluded that both genic and hormonal factors are responsible for the appearance of asynaptic meiosis in Lepidoptera.

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A survey of valvae of *Euphydryas chalcedona*, *E. c. colon*, and *E. c. anicia*

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Abstract.—A survey of male valvae of almost 500 *Euphydryas chalcedona*, *E. c. colon*, and *E. c. anicia* in western North America demonstrates that very many populations are intermediate between these entities. Six intergrading valval types are recognized, and populatons exist having each of these types as the mode. Male valvae therefore do not support treating these three as distinct species. Because wing pattern shows complex patterns, with many intermediate populations, these three entities should be treated as subspecies of *chalcedona*.

Introduction

Before 1927 the *Euphydryas* of North America, except for *E. phaeton* (Drury) and *gillettii* (Barnes) were in chaos with about 30 "species." Then McDunnough (1927) and Gunder (1929) used male genitalia to reduce the number of species to five. They include in *E. editha* (Boisduval) populations with a distinctive valva and reduced uncas with two short blunt projections. They treated *chalcedona* (Doubleday), *colon* (Edwards), and *anicia* (Doubleday) as two species, *chalcedona* (with *colon*) and *anicia*, which all have a bifid uncas with two curved claw-like hooks. *E. chalcedona* and *colon* were found to have the same short dorsal valval process, whereas *anicia* was found to have a longer process. Their treatment has been followed more or less unchanged until now, although Bauer (1975) treats *colon* as a distinct species.

I recently collected populations with male valvae intermediate between *chalcedona-colon* and *anicia*. This paper is a detailed survey of male valvae, concentrating on areas where intermediates in valvae or wing pattern occur. It proves the existence of numerous populations over a large area that are intermediate in valvae. This, together with other published evidence, leads me to conclude that *colon* and *anicia* both belong to the highly polytypic polymorphic species *chalcedona*.

Methods

Males of each population were examined and tabulated in Table 1 according to best resemblence to the drawings in Fig. 1. The dorsal wing pattern was rated in Table 1 according to whether the overall appearance is blackish, whitish, or reddish. There are numerous other wing characters involved (Hovanitz & Le Gare 1951) which this paper does not consider.

Results and Discussion

The samples fall into three arbitrary categories: *chalcedona-colon* (mostly a or b of Fig. 1), *anicia* (mostly e or f), and intermediates between the two (c or d). Some samples have a the usual form, others hav b, c, d, e, or f (Table 1). There are clearly many intermediate populations. These occur almost everywhere between the ranges of *chalcedona-colon* and *anicia,* including California, Arizona, Nevada, Washington and Montana. They are probably found in Idaho, Oregon, and British Columbia also (intermediate populations are reported for the Wallowa Mts. Oregon.) McDunnough's *paradoxa* from B.C. has somewhat intermediate genitalia (McDunnough 1927). In wing pattern the *chalcedona* and *colon* samples are very similar, black with cream spots. The *anicia* samples are usually some shade of reddish or cream-colored, rarely blackish. The intermediate genitalia samples have every type of wing pattern, and many of the populations are polymorphic in wing pattern, as are some of the *anicia* samples. The large number of samples intermediate in valvae proves conclusively that valvae cannot be used as the basis for dividing the populations into separate species.

Turner et al. (1961) show that genitalia differences do not necessarily inicate separate species are involved. They showed that the phenotype of *Papilio dardanus* Brown with a long process on the valva is due to a dominant gene, whereas the phenotype with a short process is due to its homozygous recessive allele.

A character mentioned by Bauer (1961), the minute spines on the upper process, is not useful. All samples have the dorso-posterior rim of the upper process with minute teeth. The teeth are dense on short processes and less dense on longer processes as if the same number of teeth are spread over a larger area. Associated with a long upper process is a slightly longer lower process having a reduced anterior bump. This bump sometimes is formed into a separate lobe making a bifurcate lower process, frequent in ssp. *quino* (Behr).

Gradual clinal changes in the proportions of valval forms seem to occur in some geographic areas, whereas more abrupt changes seem to occur in other areas. This is also true of the wing pattern, which is almost hopelessly complex, making the use of subspecies very dubious. Jewett (1959) accordingly suggested that further naming of subspecies be stopped.

The most reasonable interpretation of the genitalic intermediates is that of only one polytypic polymorphic species, *chalcedona.* The name *chalcedona* has page priority over *anicia,* being named on Fig. 1 versus Fig. 2 for *anicia* in the same paper.

Bauer (1975) states that in several places *colon* is sympatric with *chalcedona* and *anicia,* although these places are not stated or the statements documented. However, I cannot distinguish genitalia of *chalcedona* from *colon* and suspect that apparent cases of sympatry really are polymorphisms. Certainly such cases, if they exist, should be fully investigated and the results published. Populations only a few hundred meters from each other may exchange very few individuals and fluctuate in population size independently (Ehrlich et al. 1975), so the occurrence of two forms in the same region does not necessarily prove that they are distinct species.

The larval web character of *colon* cited by Bauer (1975) is not diagnostic because *chalcedona* and *anicia* also have webs. *E. c. capella* (Barnes) webs its *Penstemon* hostplant so extensively that defoliated plants look as if a nylon stocking had been placed over them. Dammers (1940) and Bauer (1975) state that *colon* has whiter larvae than *chalcedona* although Bauer states that *colon colon* has less white on the body than some other populations.

The one-species interpretation has also been suggested by previous work. Lionel Higgins (pers. comm.), in an unpublished study done many years ago, was not able to define the species to his satisfaction using genitalic characters. McDunnough (1927) showed that his *"colon" paradoxa* McDunnough has a longer dorsal valval process than does *"colon" perdiccas* (Edwards) and has redder wings, both traits tending toward *anicia;* wing pattern of *paradoxa,* and of *anicia* from Keremeos B. C., is identical. The original description of *wallacensis* Gunder (Gunder 1928a), previously placed in *colon* by Bauer (1975), states "genitalia of this race approach the *anicia* group" and "this race probably represents a connecting link as Dr. McDunnough has suggested." The holotype of *irelandi* Gunder has intermediate genitalia and was placed in *anicia* by Gunder (1929) and dos Passos (1964), in *chalcedona* by Bauer (1975). Gunder (1928b) described red versus white or black forms connected by intergrades for two populations [*mcglashanii* (Rivers) black, *truckeensis* Gunder red; *olancha* (Wright) whitish, *georgei* Gunder red]. The genitalia figure of *georgei* by Gunder (1929) is intermediate. Dammers (1940) successfully hybridized and backcrossed *chalcedona* and *kingstonensis* Emmel and Emmel which are very different in appearance. *E. c. hermosa* (Wright) was placed in *anicia* by Gunder (1929) and Bauer (1975), but in *chalcedona* by dos Passos (1964) and Emmel and Emmel (1972); *kingstonensis, klotsi* dos Passos, *hermosa,* and *morandi* Gunder all have very similar wing pattern, yet have been placed in several "species." Bauer's (1975) subspecies of *"colon"* from Elko Co. Nevada is stated to have white, red, and black forms. Red populations from California (*sierra* [Wright]) and Arizona (*klotsi*) have been included among the west coast black populations in the same species *chalcedona* by Gunder (1929), dos Passos (1964), and Bauer (1975). Finally, dos Possos (1964), McDunnough (1927), and Gunder (1929) treated *colon* and *chalcedona* as conspecific.

In many places in the intergradation zone in western U.S. the male valvae change from one form to another at a different place than the wing pattern. Wing patterns change in regions where valvae do not (many places), and valvae change in regions where wing patterns do not (such as in British Columbia, Arizona, and Nevada). This phenomenon of non-concordance of characters is typical of many polytypic species, such as for wing characters of *Speyeria callippe* (Boisduval) (Hovanitz 1943). When separate species are involved most characters usually change at the same place.

Higgins (1978) has split the genus *Euphydryas* into four separate genera,placing *editha, chalcedona, c. colon,* and *c. anicia* into *Occidryas* Higgins; I prefer to treat these names as subgenera to avoid the awful fate of the birds, in which each species is in its own genus.

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TABLE I

Number of individuals of each valval type (a to f of Fig. 1), and predominant wing color and subspecies, for each locality.

Locality	a	b	c	d	e	f	Main Color	Subspecies
Jerseydale, Mariposa Co. Calif.	-	-	1	-	-	-	black, cream	chalcedona
Indian Flat, Mariposa Co. Cal.	-	2	-	-	-	-	black, cream	chalcedona
El Portal, Mariposa Co. Cal.	1	-	-	-	-	-	black, cream	chalcedona
Lang Crossing, Nevada Co. Ca.	2	1	-	-	-	-	black, cream, red	chalcedona
Foote Crossing, Sierra Co. Ca.	1	2	-	-	-	-	black, cream	chalcedona
Blue Ravine, Sierra Co. Ca.	-	-	1	-	-	-	black, cream, red	chalcedona
Fiddle Crk., Sierra Co. Ca.	-	1	1	-	-	-	black, cream	chalcedona
Whiskeytown Res., Shasta Co. Calif.	5	4	1	-	-	-	black, cream	chalcedona?
Cedar Pass, Modoc Co. Ca.	-	1	-	-	-	-	black	colon
SE Copper, Siskiyou Co. Ca.	3	4	1	1	-	-	black, cream	colon?
Kinney Crk., Jackson Co. Ore.	-	2	-	-	-	-	black, cream	colon?
French Gulch, Jackson Co. Ore.	1	1	-	-	-	-	black, cream	colon?
Illinois R. rd., Josephine Co. Ore.	-	1	-	-	-	-	black, cream	colon?
Wolf Creek, Josephine Co. Ore.	1	2	-	-	-	-	black, cream	colon?
Bly Mtn., Klamath Co. Ore.	4	4	1	-	-	-	black, cream, red	colon-dwinellei Hy. Edw.
S. La Pine, Klamath Co. Ore.	1	-	-	-	-	-	black, cream	colon-dwinellei
Odell L., Klamath Co. Ore.	2	1	-	-	-	-	black, cream	colon?
Hart L., Linn Co. Ore.	1	-	-	-	-	-	black, cream	colon
Monument Pk, rd. Linn Co. Ore.	1	1	-	-	-	-	back, cream	colon

Cascadia, Linn Co. Ore.	1	-	-	-	-	-	black, cream	colon
Cascadia S. Park, Linn Co. Ore.	1	-	-	-	-	-	black, cream	colon
nr. Halfway, Baker Co. Ore.	-	3	1	-	-	-	black, cream	wallacensis
Lost Prairie, Linn Co. Ore.	-	1	-	-	-	-	black, cream	colon
SE Drew, Douglas Co. Ore.	-	1	-	-	-	-	black, cream	colon
McDonald Forest, Benton Co. Ore.	1	-	-	-	-	-	black, cream	colon

Locality	a	b	c	d	e	f	Main Color	Subspecies
Siskiyou Summit, Jackson Co. Ore.	2	1	-	-	-	-	black, cream	colon
Satus Pass, Yakima Co. Wash.	-	1	-	-	-	-	black, cream, some red	paradoxa?
Hurricane Ridge Clallam Co. Wash.	8	3	-	-	-	-	black, cream	perdiccas
Tucannon R., Columbia Co. Wash.	1	-	-	-	-	-	black, cream	wallacensis
Horse Crk., Wallowa Co. Ore.	1	-	-	-	-	-	black, cream	wallacensis
Camas Prairie, Sanders Co. Mont.	-	2	-	-	-	-	black, cream, some red	wallacensis
Gilbreth Spgs., Columbia Co. Wash.	-	-	1	-	-	-	black, cream	wallacensis
9-mile Crk., Missoula Co. Mont.	-	-	2	-	-	-	black, cream	wallacensis
Pattee Can., Missoula Co. Mont.	-	-	2	4	-	-	black, cream	wallacensis
Miller Crk., Missoula Co. Mont.	-	1	10	17	8	-	black, cream	wallacensis
Warm Spgs. Cgd., Ravalli Co. Mont.	-	-	-	1	-	-	black, cream, red	howlandi S. & T.?
Ronan, Lake Co. Mont.	-	-	-	1	-	-	cream, black	bernadetta?
SE Easton, Yakima Co. Wash.	-	1	1	2	-	-	some black, some red-cream	hopfingeri Gunder?
Peoh Peak, Kittitas Co. Wash.	1	1	-	4	-	-	black, cream	paradoxa?
Rush Creek, Washoe Co. Nev.	-	-	-	12	8	1	cream, black, some red	veazieae F. & J.
N. Hallelujah Jct. Lassen Co. Cal.	2	5	3	1	1	-	black, cream, some red	veazieae-sierra?
Bartle, Siskiyou Co. Cal.	-	2	2	-	-	-	black, forewing reddish	dwinellei
Kin Can., Ormsby Co. Nev.	-	4	3	1	-	-	cream, black, sl. red	olancha-sierra?
Loon Lake, El Dorado Co. Ca.	-	14	8	3	-	-	red to black, sl. cream	sierra
Sonora Pass, Tuolumne Co. Calif.	-	-	-	1	2	2	black-cream-red	sierra-olancha
Ebbets Pass, Alpine Co. Ca.	-	-	-	1	-	-	red	sierra
Hermit Valley, Alpine Co. Calif.	-	-	1	-	-	-	red	sierra
Echo Lake, El Dorado Co. Ca.	1	2	1	2	-	-	red	sierra

Carson Pass, Alpine Co. Ca.	9	16	19	5	1	-	red to black, mixed	sierra?
Big Pine Mdw., Tulare Co. Calif.	3	9	3	-	-	-	cream, some red-black	olancha?
Oak Crk. Can., Coconino Co. Ariz.	-	1	2	5	-	-	ochre, some black-cream	klotsi
N. Canyon, Yavapai Co. Ariz.	-	-	3	-	-	-	ochre, some black-cream	klotsi
Yava, Yavapai Co. Ariz.	-	-	2	-	-	-	ochre, some black-cream	klotsi

Locality	a	b	c	d	e	f	Main Color	Subspecies
Providence Mts. San Bern. Co. Calif.	-	2	10	1	-	-	ochre	kingstonensis
Rock Corral, San Bern. Co. Calif.	1	1	2	-	-	-	red	corralensis E. & E.
E. Jacumba, San Diego, Co.Ca.	-	1	3	1	-	-	cream, black	quino
W. Jacumba, San Diego Co. Ca.	-	2	2	-	-	-	cream, black	quino
E. Jacob Lake, Coconino Co. Ariz.	-	-	-	-	1	1	ochre	hermosa?
Peppersauce Can., Pima Co. Ariz.	-	-	-	-	2	1	ochre	hermosa
Horseshoe Cienega, Apache Co. Ariz.	-	-	-	-	2	3	ochre-red-black cream	magdalena B. & McD.
Mt. Wheeler Scenic Area, White Pine Co. Nev.	-	-	-	-	-	2	red, cream	wheeleri
Austin Summit, Lander Co. Nev.	-	-	-	-	-	1	red, cream	wheeleri
W. Durkee, Baker Co. Ore.	-	-	-	-	2	-	white, some red	bakeri S. & T.
Trout Crk. Rd., Harney Co. Ore.	-	-	-	-	1	1	white, some red	macyi F. & J.
Wildhorse Crk., Harney Co. Ore.	-	-	-	-	-	1	white, some red	macyi
Salmon Mdws., Okanogan Co. Wash.	-	-	-	-	2	2	black, red, cream	hopfingeri
Humphrey, Clark Co. Idaho	-	-	-	-	-	1	black, red, cream	howlandi?
Swan L., Madison Co. Mont.	-	-	-	-	-	3	black, red, cream	howlandi?
S. Norris, Madison Co. Mont.	-	-	-	-	2	5	cream, black	bernadetta Leussler
4 Mile Crk., Sweet Grass Co. Mont.	-	-	-	-	1	-	red, some black-cream	windi Gunder?
5 mi. S. Wasa, B.C.	-	-	-	-	1	1	red, some black-cream	anicia
Ft. Steele, S. Wasa, B.C.	-	-	-	-	-	2	red, some black-cream	anicia
Elko, B.C.	-	-	-	-	2	3	red, some black-cream	anicia
8 mi. W. Cranbrook B.C.	-	-	-	-	-	1	red, some black-cream	anicia
Halfmoon Park, Sweet Grass Co. Mont.	-	-	-	-	-	1	cream, black	bernadetta

Swamp Crk., Sweet Grass Co. Mont.	-	-	-	-	-	1	cream, black	bernadetta
McLeod, Sweet Grass Co. Mont.	-	-	-	-	3	5	cream, black, red	howlandi?
Polaris, Beaverhead Co. Mont.	-	-	-	-	5	5	cream, black, red	howlandi
Bozeman, Gallatin Co. Mont.	-	-	-	1	2	4	cream, black, red	howlandi
Gallatin Mts., Gallatin Co. Mont.	-	-	-	-	1	6	cream, black, red	bernadetta-howlandi
Bridger Can., Carbon Co. Mont.	-	-	-	-	1	1	cream, black, red	same
Mile 154, Haines Jct., Yukon	-	-	-	-	3	1	red, black, cream	helvia Scudder

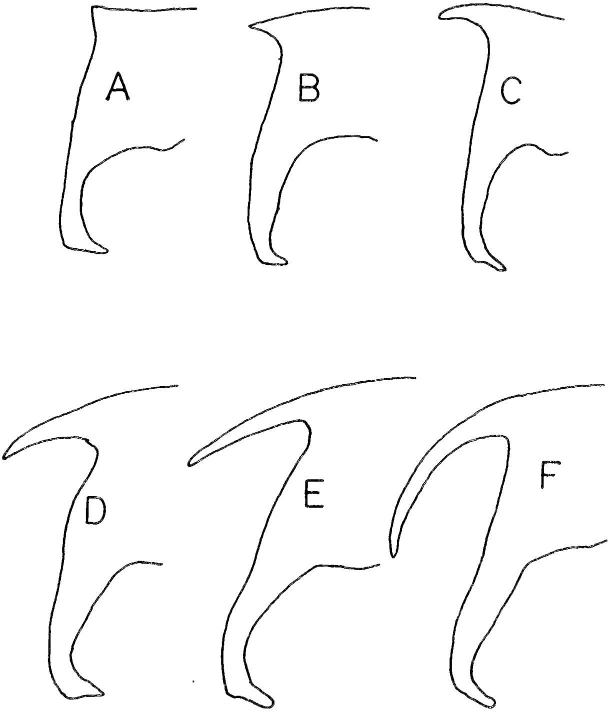

Figure 1. Six shapes of the valval process in *Euphydryas chalcedona*, *E. c. colon*, and *E. c. anicia* used in Table I.

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Notes on Maryland Lepidoptera No. 7: Eight new butterfly records for the state of Maryland

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Our continued study and research on Maryland butterflies has become progressively more difficult due to the massive destruction of the habitats: forest and field alike, and even the vast salt marshes, the last of which had always seemed indestructable. However, our field work eventually either turns up something new or assists in reevaluating old records.

1. *Papilio cresphontes cresphontes* (Cramer) has been known from Maryland for many years. Although *P. C. cresphontes* is occasional throughout the state, the largest colony exists along the Potomac River valley, especially from Cabin John, Montgomery County, Northwest to Little Orleans, Allegany County. Here the spring brood (May) is indistinguishable from *Papilio cresphontes pennsylvanicus* (Chermock and Chermock). Later on the summer broods are typical *cresphontes.* In such a situation one cannot justifiably call the spring brood true *pennsylvanicus,* but it is noteworthy to record this condition for future resolution.

2. Our good friend Dr. John Mason went collecting with his family April 9, 1968, along the Potomac River. Near Dargan, Washington County, he discovered a small colony of the dark spring form *Celastrina pseudargiolus nigra* (Edwards). Aware the Harry Clench of the Carnegie Museum was working on this species, Mason forwarded some specimens to Clench. He incorporated the material into a paper naming the dark form as a distinct cryptic species — *C. ebenina* (Clench, 1972). We have visited the area in the spring and also collected *ebenina* but very sparingly (one a season). Males are rare, but females are extremely rare. (Only two females have been captured in the area.) The known flight period here is April 9 to April 27th. Dr. Mason feels this butterfly flies every year but it is definitely more common every other year.

3. Our long search for *Strymon acadica* (Edwards) has always met with failure. On July 10, 1972, our friend Phil Kean collected a large fresh female on the campus of University of Maryland, Baltimore County. The hairstreak was busy feeding on the flowers of burdock *(Arcium)* in an open field not far from Willow (*Salix* sp.). The capture establishes a first known Maryland record. Phil kindly donated the specimen to W.A.A.

4. We have suspected the presence of *Strymon caryaevorus* (McD.) in Maryland for many years and believe we have collected it annually in Garrett County since 1950. When Mr. Frank Chermock examined the genitalia of specimens we had collected July 10, 1958, near Grantsville, their identity was confirmed as *S. caryaevorus* and *S. falacer* (Godart).

5. When visiting Dr. John Mason he casually asked us about good collecting areas in Maryland. We suggested that for overall collecting Charles County was an excellent spot, especially around Liverpool Point.

Armed with this information Dr. Mason and his family, all collectors, headed for Liverpool Point on August 23, 1973. They collected many butterflies that day, but never completely identified the catch. We later inspected this collection and were very surprised to find a beautiful fresh female *Hesperia attalus* (Edw.). Here we sent John to our best collecting area which we had thoroughly collected for the past ten years, but evidently we had not worked it enough. John came up with one of the country's rarest butterflies. We have collected the area many times since and have never seen this rare butterfly. Dr. Mason, in his usual kind way, gave us the specimen for our collection.

6. Next to Dr. John Mason's *Hesperia attalus* were four *Lerodea eufala* (Edw.) also from Liverpool Point on August 23, 1973, and also a new species from Maryland which we have been trying to find for years. John gave us two of the specimens.

7. We recently described a new subspecies of *Poanes massasoit* (Scud.) from deep Eastern Shore territory of Maryland (Andersen and Simmons 1976). We named the butterfly after our dear departed friend, Franklin Chermock, who was not only a great lepidopterist but a rare kind gentleman.

Although the description of *Poanes massasoit chermocki* (Andersen and Simmons) was published, it is included herein to formally add the butterfly to the list of Maryland butterflies.

8. Austin Clark (1932) reported and described a new subspecies of *Poanes massasoit* from Beltsville, Maryland - *P. massasoit hughi* (Clark). The Beltsville area lies in the Fall Line and on the Coastal plain.

When Clark published his "Butterflies of the District of Columbia" in 1932, he incorporated the Beltsville colony reporting the butterfly as *P. massasoit massasoit.* However, he later described this colony as *P. massasoit hughi.* Therefore, *P. massasoit massasoit* has not been published as an indigenous butterfly for Maryland.

For many years we have been collecting *P. massasoit massasoit* from the more northern parts of Maryland, including Baltimore, Carroll, Harford, and Howard Counties. A possible factor of subspeciation may lie in the clines from Coastal Plain and Fall Line to the Piedmont areas.

The summarized data follow:

Species	Date	Locality
1. *Papilio c. pennsylvanicus*	V-15-58	Little Orleans, Allegany Co., Md.
2. *Celastrina ebenina*	IV-27-75	Dargan, Washington Co., Md.
3. *Strymon acadica*	VII-10-72	Univ. of Md. Campus, Balto. Co., Md.
4. *Strymon caryaevorus*	VII-10-58	Grantsville, Garrett Co., Md.
5. *Hesperia attalus*	VIII-23-73	Liverpool Point, Charles Co., Md.
6. *Lerodea eufala*	VIII-23-73	Liverpool Point, Charles Co., Md.
7. *Poanes m. chermocki*	VII-12-62	New Bridge, Dorchester Co., Md.
8. *Poanes m. massasoit*	VII-15-54	Eklo, Balto. Co., Md.

Notes on Maryland Lepidoptera No. 8:

Erora laeta (Edw.)

Almost all members of the select *Erora laeta* club have agreed on one axiom for finding this rarest of species. "It occurs in the most unlikely place when least expected."

We have been researching the butterflies of Maryland for many years. A list is maintained of at least twenty probable species that we have been constantly trying to discover somewhere in Maryland. One of our prime targets has always been *E. laeta,* the rarest butterfly in the Eastern U.S. Every reported capture of *E. laeta* has been followed very carefully and every detail scrutinized with the hope of finding some clue that would help us locate this species in Maryland. This butterfly is usually confined to the Canadian Zone Forest. The only Canadian Zone in the state of Maryland is in the westernmost part of the state - mountainous Garrett County.

On May 3, 1956, Harry K. Clench was collecting in Powdermill Nature Reserve near Rector, Pennsylvania. He was very fortunate to collect one male *E. laeta.* Rector is within twenty-five miles of the Garrett County Canadian Zone area of Maryland. With this new knowledge and renewed vigor we again plowed through the mountains of Garrett County to no avail.

On April 9, 1968, Dr. John Mason discovered a colony of *Celastrina ebenina* (Clench) near Dargan, Maryland. This area lies in the Potomac River valley not far from Harpers Ferry, West Virginia, about as far as you can go from Canadian Zone. In the spring of every year we work this area for *C. ebenina.* We usually wind up catching one or two a year, for they seem to be rare here. During the spring of 1977 we attempted to find *C. ebenina* in new areas other than the first discovered colony.

On April 14, 1977, we checked areas closer to the Potomac River. We came upon a small open dirt area beside the road. The dirt area was surrounded by climax forest and contained two small puddles which looked ideal for *C. ebenina.* We very slowly and carefully checked every inch because *C. ebenina,* being dark, is difficult to spot. On the far side of one of the puddles R.S.S. spotted a dark specimen just sitting. He instantly put his net over the specimen, for how many times do we try to make a sure identity before capture and by the time the identity is made the specimen is gone. This time the specimen was caught first and identified second. As we both rushed to see the sex of the *C. ebenina* we went into rapture at the sight of a fresh male *E. laeta.* R.S.S. was certain that if he had known the true identity he would have definitely thrust the net at least six inches into the ground.

We thoroughly searched the area that day and other days but found no more. It was a very tough area to collect. Aside from the small clearing where we caught *Erora laeta* the entire area is on a steep wooded slope.

On seeing the butterfly the first time in the net the wings were slightly expanded. The color seemed too dark for *C. ebenina* so we checked the underside. This is when we knew we had *Erora laeta.* However, the red spots on the bottom were very faint. Most of the *E. laeta* illustrations show ventral red spots and a bright blue butterfly dorsally. Our specimen was black with only a slight bit of blue showing.

Did we have a possible subspecies? At the National Museum of Natural History we examined the *E. laeta* series. The males were very much like ours. The bright blue specimens were the females and even some females were rather dark. With this in mind the collector should not be looking for *E. laeta* in the spring as a blue butterfly since seventy-five percent of them are dark.

We are still sure *Erora laeta* exists in the Canadian Zone of Western Maryland and hope to locate some in the future.

Some facts that could be pertinent are the associated species. Our *E. laeta* was flying at the tail end of a *Celastrina argiolus pseudargiolus* (Boisduval and LeComte). and with *Lycaena phlaeus americana* (Harris).

Glaucopsyche lygdamus nittanyensis (Chermock) were fresh while *Erynnis juvenalis* (Fabricius) were slightly worn. The spring zebra swallowtail *Graphium marcellus* (Cramer) were also worn. *Papilio troilus* (Linnaeus) were fresh. This flight period information should be a clue as to when to look for *E. laeta.*

Notes on Maryland Lepidoptera No. 9: Seven new butterfly records for the state of Maryland

Our continued study of Maryland Lepidoptera is often greatly assisted by fellow collectors usually covering new areas or areas where we have not concentrated our collecting.

1. Mr. Elra Palmer of Baltimore kindly gave the senior author a few Maryland butterflies from his collection.

Much to the senior author's surprise there was a California Dogface Sulphur butterfly, *Colias elirydice* (Bois.) among the group. The specimn was collected on July 6, 1933 at Deal Island, Somerset County, Maryland. The butterfly was collected by a beetle collector who did not know Lepidoptera. He saw the specimen on a flower and thought it was unusually colorful, whereupon he took it for his friend, Elra Palmer, a butterfly collector.

How the butterfly got to Maryland is a mystery. One guess would be that the crysalis was on a plant bought in California, shipped to Maryland and he crysalis hatched upon destination.

This record is not published as an indigenous species but rather as a curiosity. (ed. it may be a convergent aberration.)

2. During two consecutive summers in the sixties the senior author visited Ocean City, Maryland, during August. On both occasions he was playing checkers under a beach umbrella. Along came a Gulf Fritillary, *Agraulis vanillae nigrior* (Michener) which slowly fluttered under the umbrella toward the red checker board. On realizing the red was not a flower, the butterfly took off up the beach with great speed making capture impossible. The senior author was quite frustrated since there are no legitimate records from Maryland and sight records are not reliable.

However, on August 15, 1978, Mr. William Grooms collected two specimens five miles north of Salisbury, Maryland, on the Eastern Shore. They were fighting while flying along a dirt road and were netted in mid-air.

The capture certifies the senior author's sightings and represents the first Maryland records. Bill very kindly gave us a specimen for our collection.

3. *Erynnis persius* (Scud.), has been recorded for Washington, D.C., by Clark (1932). However, he confused this butterfly with *E. baptisiae* (Forbes). Dr. John Burns, working with this group, could find no Maryland records in the Smithsonian collection. However, he did identify a male *E. persius* in the junior author's collection that was collected on May 12, 1955, at Piney Grove, Allegany County, Maryland. This record constitutes the first known Maryland capture.

4. On August 23, 1979, Mr. William Grooms collected a fresh *Oligoria maculata* (Edw.) on fresh blossoms of Hercules Club, *Araua spinosa* near Seneca, Montgomery County, Maryland. The Hercules Club was located along the edge of a deciduous forest. This represents the first known specimen from the state of Maryland. Bill was very kind to give us the specimen for further study.

5. Mr. William Grooms collected a fresh *Polites v. vibex* (Geyer), on fresh flowers of Hercules Club, *Araua spinosa* on August 30, 1979, within the town limits of Lexington Park,St. Mary's County, Maryland. The Hercules Club was also at the margin of a woods.

This specimen is the first known of its kind from the state of Maryland and again Bill was kind enough to donate the specimen to our studies.

6. Dr. John Glaser of Baltimore made a field trip to Dorchester County, Maryland on July 23, 1979. He was actually in search of *Poannes viator* (Edwards) and *Poannes aaroni* (Skinner.) Near the

town of Robbins he found some flowering swamp milkweed on which he collected two skippers. After a close examination they proved to be a worn pair of *Problema byssus* (Edw.) The species is one we have been trying to discover for years and constitutes the first Maryland record.

7. Mr. Franklin Chermock had collected *Calpodes ethlius* (Stoll) in great numbers in Florida. He therefore was aware of its habits and the tactics of its larva.

On August 16, 1956, walking near some large Canna beds near Druid Hill Park in Baltimore, he thought he saw some typical larva shelters on the plants. He examined some of the Canna plants and discovered many larvae in all stages of development. After finding several full grown larvae they were taken home to pupate and emerge. These hatched into *C. ethlius,* which has been reported previously in Washington, D.C. (Clark), but this is the first Maryland record.

The summarized data follow:

Species	**Date**	**Locality**
1. *Colias elirydice*	VII-6-33	Deal Island, Somerset County
2. *Agraulis vanillae nigrior*	VII-15-78	Hebron, Wicomico County
3. *Erynnis persius*	V-12-55	Piney Grove, Allegany County
4. *Oligoria maculata*	VIII-23-79	Seneca, Montgomery County
5. *Polites v. vibex*	VIII-30-79	Lexington Park, St. Mary's County
6. *Problema byssus*	VII-23-79	Robbins, Dorchester County
7. *Calpodes ethlius*	VIII-16-56	Baltimore City, Maryland

Literature Cited

Andersen, W.A., and Simmons, R.S., (1976). Contribution #5. Notes on Maryland Lepidoptera. A new subspecies of *Poanes massasoit* (Hesperiidae). Journal of Lepid. Soc. 30 (1) 19-22.

Journal of Research on the Lepidoptera 17(4): 260-264, 1978(80)

Review

Ferguson, D. C., *in* Dominick, R. B., *et al.*, 1978, The Moths of America North of Mexico, Fasc. 22.2, Noctuoidea (in Part): Lymantriidae. E. W. Classey Ltd. and the Wedge Entomological Research Foundation, 1978. $48.00 (Subscription $40.00). Distributed in USA and Canada by Entomological Reprint Specialists, P.O. Box 77224, Dockweiler Station, Los Angeles, CA 90007. Date of publication 25 March 1978.

This fascicle, often advertised as soon appearing, and eagerly awaited, finally did. The Lymantriidae are a very difficult family and many relationships had to be elucidated to make the publication useful: names, distribution and general considerations.

Retention of the family name is to be lauded as well as other often applied generic names which have been unstable in the past because of international faunal and taxonomic complications. Examples include *Gynaephora, Dasychira, Lymantria, Leucoma* and *Euproctis.* Appreciable conservatism is also shown in specific names, e.g. *Euproctis chrysorrhoea.* One may hope that the final nomenclature of Ferguson finds easy access into our collections and papers.

One important question arises as to whether it was necessary to fill the literature with all the new "subspecific" names. Additional biochemical and larval taxonomic research would probably obliterate some of the "subspecies" and show them to be species in their own right. Here is certainly a field open for further research.

In general the keys are good because they are short, useful and workable. The larval key to the last instar larvae of *Orgyia,* however, leaves a general question open. Can a larva of a "subspecies" be described when the so-called "type" of this "subspecies" is questionable ("*leucostigma plagiata*") and the larvae in question do not yield adults agreeing with this "type"? Otherwise the key is helpful and correct.

Dasychira is certainly the most difficult genus, and Ferguson, whom we know was especially involved over decades with this genus, can take pride in the fruits of long labor. The explanations concerning the generic name finally make *Dasychira* definitive for our species. Also we congratulate Ferguson for his success in re-defining *D. tephra.* Following the latter conclusion everything else falls in place. We are also thankful that he was able to confirm and give new meaning to names and taxa so familiar to all of us, but which were previously so often doubted by overzealous workers: *obliquata, cinnamomea,* *atrivenosa, meridionalis, basiflava, leucophaea, dorsipennata, plagiata* and *grisefacta.* Other names such as *aridensis, parallela, lemmeri, pini* disappeared, after having contributed much confusion in the past.

The other difficult genus in the family is *Orgyia.* Regretably one can not say what was just said about *Dasychira* in this case. The good points of the treatment include:

a) Confirmation that all included North American species belong to one well-defined genus, *Orgyia.*

b) Confirmation of *O. cana* as a species in its own right. The latter, however, is not a "revised status," as it was already treated as such in *Entomol. Zschr.* 83: 12, in 1973, a publication omitted from the citations. Problems with associations of *Orgyia* larvae would have been completely and easily resolved if Ferguson had used the preserved and associated larvae and adults from the McFarland rearings (Los Angeles County Museum of Natural History). It should be reiterated that MONA authors seem to rely too exclusively on the collections of the United States National Museum, an objection Rindge raised in *Journ. Lep. Soc.* 28: 4.

c) Giving taxonomic status to the puzzling very large California *Orgyia* (*magna*), although further research is quite necessary.

d) Detection of the old Boisduval specimen in the collection of the United States National Museum which Guerin-Meneville figured and used for the name of *O. detrita.* It should be remarked that "Degens Bd. Am. B." is not "apparently . . . an unpublished name" but is Latin for "coming from Boisduval America Borealis" (the Latin verb is dego, -i, -ere).

e) Additional knowledge about *O. falcata* and its larva.

The negative side includes the following points:

a) The laconic statement "the female genitalia have not been studied." Besides the fact that they have been very extensively studied and reported in several issues of *Entomol. Zschr.,* the female genitalia are of decisive taxonomic importance in the genus *Orgyia.* For a "definitive" presentation of North America moths the attitude is not quite understandable.

b) Omission of observations about pupae is likewise not quite understandable, the more so as the form of the pupae also appears as important specifi characteristic.

c) Omission of any study of the eggs by scanning electron miscroscopy and electrophoresis as well as important larval characters, such as mandibles, ocelli, setae on thoracic legs, headcapsules and surface of exterior cuticle.

d) Claiming of a "new synonymy" for *O. definita kendalli* on p. 75 when the synonymy (*definita kendalli* = *leucographa*) was earlier established in *Entomol. Zschr.* 83: 14 (1973).

e) Establishing of "new status" in the *rindgei/leuschneri* complex while Chua *et al.* had already published specific status for *O. rindgei* in *Journ. Res. Lep.* 15: 4 (1976). The treatment was repeated by Riotte in *Entomol. Zschr.* 87: 3 (1977).

Some special words have to be directed to the "enfant terrible" of the whole fascicle, *O. leucostigma.* As Ferguson presents it, it appears to make sense. The realities, however, are otherwise:

a) The aedoeagus which he says "may be at once distinguished from all other species in that it is apically tapered to a point" is blunt and not tapered to a point, as SEM micrographs show.

b) The (not studied) female genitalia would have helped to another, and perhaps more correct, classification.

c) Use of the earlier pusblished results of egg electrophoresis would have shown that indeed *leucostigma* is extensively sympatric with *wardi* which in no way can be regarded as a "subspecies" or "synonym" of anything.

d) Larval structures, if they had been used, would have shown the same (they also have been published previously).

e) To use the so-called "Walker type" of *Acyphas plagiata,* abdomenless as it is and without any locality label, as type for a "subspecies" of *leucostigma* in Nova Scotia, replacing *wardi,* is absurd at best. Insect pins may be convincing sometimes, but in a case like this, certainly not. The Walker specimen could be used for the real *leucostigma* in Nova Scotia, but I can see no need for such a designation. Competent workers in the British Museum came to a quite different evaluation of the Walker specimen and placed it together with *leucostigma* from Wisconsin as the best match. Therefore, one should list the Walker type as "incertae sedis". One good point should be mentioned in this regard; with Abbot's larval painting of *leucostigma* declared as lectotype of the species, we have a good basis for its definition. It would also appear that the male figure of Abbot's *leucostigma* is really *definita.* (Many of Abbot's plates are mixed with non-conspecific creatures.)

Ferguson's final treatment of the *leucographa* Geyer problem is good and without objection.

The plates in this volume are of the expected quality and the depicted specimens rich and very useful. The only thing we miss is a single specimen of *Orgyia wardi* from the type locality (Prospect Road, Nova Scotia). *O. wardi* would be best figured with a *leucostigma* from the same locality to show the difference. The Nova Scotia specimens figured are all *leucostigma.*

Missing from the literature cited is the important paper by Chua *et al.*, 1976, Investigation of selected species of the genus *Orgyia* (Lymantriidae) using isoelectrofocusing in thin layer polyacrylamide gel, (*Journ. Res. Lep.* 15 (4): 215-224) as well as Riotte, 1973, Uber *Orgyia* (*O.*) *gulosa* und *Orgyia* (*O.*) *cana* (Lep: Lymantriidae), (*Ent. Zeits.* 83 (12): 129-140), and by the same author, 1977, Abschliessende Bemerkungen zu den Studien uber nordamerikanische Arten der Gattung *Orgyia* (Lep.: Lymantriidae), (*Ent. Zeits.* 87 (3): 9-12) concerning *definita, rindgei* and *leucographa* = *detrita.* The above ommissions do not otherwise interfere with the great value of the fascicle. We certainly welcome its final appearance and wish it long-lasting success.

To clarify the question of sympatric occurence of *wardi* and *leucostigma* in Nova Scotia, we include illustrations of both from the type Prospect Road locality. The former was reared from a blackish-brown-headed larva on larch; the latter from a cinnabar red-headed larva on alder. We also present an illustration of the type of *Acyphas plagiata* Walker which shows relationships to the Nova Scotia *leucostigma* specimen, however, not to the specimen of *wardi.*

J. C. E. Riotte, Research Associate, Department of Entomology, B. P. Bishop Museum, Honolulu, Hawaii, and Royal Ontario Museuem, Toronto, Ontario.


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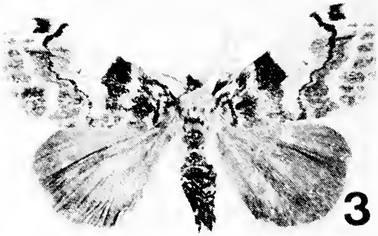
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Fig. 1 type specimen of Ancypha plagiata Walker in the British Museum (Nat. Hist.); fig. 2 *Orgyia leucostigma* from Milwaukee, Wisconsin, 20 Aug. 1915, H. M. Bower; fig. 3 *Orgyia leucostigma* from Sudbury, Ontario, ex ovo, 16 Jul 1961, on maple; fig. 4 *Orgyia leucostigma* from Toronto, Ontario, ex ovo, 26 Aug 1974, on maple; fig. 5 *Orgyia leucostigma* from Kingston, Ontario, ex ovo, 24 Jul 1971, on maple; fig. 6 *Orgyia leucostigma* from Prospect Road, Halifax, Nova Scotia, ex ovo, 21 Jul 1971, on maple and alder; fig. 7 *Orgyia wardi* from Prospect Road, Halifax, Nova Scotia, ex ovo, 23 Jul 1970, on larch.

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Response to J. C. E. Riotte's Review of the *Lymantriid Fascicle*

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The review of my lymantriid revision by the Rev. J.C.E. Riotte is not an unfavorable one, but I am glad of the opportunity to discuss a few points with which I do not entirely agree. It should be evident that the writing of a comprehensive faunal work such as *The Moths of America North of Mexico* by relatively few authors with limited technical support, if it is ever to be completed, hardly allows time to explore and evaluate such techniques as electrophoresis and scanning electron microscopy as he advocates. The techniques are good, but interpretation of the results remain questionable at this stage when we still do not know what they mean in terms of inter- or intraspecific variation in the Lepidoptera. I do not share Riotte's faith in their validity. For example, who is to say whether the variation in the reticulate pattern around the micropyle of the egg such as he illustrated (1971: 107 and elsewhere) is of specific significance? Such methods may of course yield important taxonomic evidence in a proper research context which would involve demonstrating what the variation means by examination of large numbers of specimens, but they are not practical for resolving minor problems in *Orgyia* in a work of this nature when thousands of other species remain to be treated.

The complaint that of Moths of America North of Mexico authors fascicles "rely too exclusively" on collections of the USNM is unjustified because no less than 20 collections were studied during preparation of fascicle 22.2, including that of the Los Angeles County Museum. However, I was unaware of the existence of the associated larvae that he mentions.

On the one hand Riotte approves of my conservatism (paragraph 2), but in the next paragraph says, in effect, that all those new subspecies were not worth naming because further study would probably show that some of them are really good species!

My statement, "Female genitalia not studied, was intended to mean not studied *by me.* I did see enough of them to conclude that they are not "of decisive taxonomic importance," at least not at the level where such morphological evidence is needed, i.e., for distinguishing very closely related species.

The controversy over *Orgyia wardi* Riotte persists, but after reviewing the problem again I still think that in all probability it is a mythical species. I am extremely familiar with what Riotte described as *wardi*; it is the prevalent form in Nova Scotia. The dark, blackish-headed larva characteristic of this "species" represents about 99% of the population, not only in the type-locality but probably everywhere on mainland Nova Scotia (Sable Island has a very different subspecies discovered too late to be covered in fasc. 22.2). Light, red-headed larvae tyical of *leucostigma* as it occurs from Maine southward and westward turn up in Nova Scotia relatively rarely, and the specimen I chose to illustrate on plate 7, figure 42, was reared from one of these as mentioned in the text. It would seem extremely unlikely that all six adults that I illustrated are referable to *"leucostigma"* (i.e., from pale, red-headed larvae comprising only 1% of the population) as Riotte claims. The type of *plagiata* Walker and paratypes before me of *wardi* all represent the form with a brownish submarginal band on the forewing, closely matching my figures 41 and 42. This brownish form, which may be reared from either light or dark larvae, is much commoner in Nova Scotia than elsewhere, thus providing part of the evidence that the type of *plagiata* is of Nova Scotian origin. Although Riotte considers my identification of the type of *plagiata* "absurd," even based as it was on detailed examination of the actual specimen, he does not hesitate to identify all six of my color illustrations as representing *"leucostigma"* rather than *"wardi."* I agree that they are *leucostigma* — *Orgyia leucostigma plagiata* (Walker), with *wardi* Riotte as a synonym.

Food plants mean nothing in this connection because *leucostigma* is about the closest thing to a polyphagous species that one can find. The supposed genitalic differences that Riotte figured (1971: 112) also have no significance because one can make many genitalia slides of the *leucostigma* complex and hardly find two valves alike. Neither do his figures of the female genitalia (1971: 113) show, to my eye, any clear differences. I have already commented upon "Die Mikropylrosette." I think that it will be obvious to most readers that the aedoeagus of *leucostigma* is indeed tapered to a point relative to those of other species as viewed through an ordinary dissecting microscope. Of course it could appear blunt in a SEM photograph. Riotte's larval ocelli diagrams (1971: 109) show the two largest ocelli separated in *wardi* and contiguous in *leucostigma.* I studied many larvae to check on this. Although the difference may be partly real, it is also partly and perhaps entirely an optical illusion resulting from the much greater amount of melanin in the head capsules of the dark Nova Scotian larvae. The darkened integument encroaches closely upon the ocelli and halfway up their sides, thus exaggerating the apparent space between them and minimizing their apparent size. If there is such a difference it is certainly more subtle than his illustrations indicate and presumably subspecific.

My assignment of *O. definita kendalli* Riotte to the synonymy of *detrita* was correctly indicated as "new synonymy." Riotte did synonymize it earlier, but to *leucographa*, which is a synonym of *leucostigma*. The 1976 and 1977 papers he mentions as being omitted were received too late to be considered, but the 1973 paper on *O. gulosa* and *O. cana* was for some reason missing from my file and really was overlooked. On reviewing these papers now, however, I find that they would not have changed anything taxonomically. In the last mentioned Riotte refers to the types that he figured of *gulosa* and *cana* of Henry Edwards as "Typus" and "Holotypus" respectively. Actually they were only syntypes, each name having been based on more than one specimen without a holotype mentioned. Inasmuch as Riotte faults me for neglecting pupal characters, it might be of interest to note that in the 1973 paper cited, p. 135, he illustrates pupae of *gulosa* and *cana* in such a way that one is left to assume that the very great differences aparent between them are of specific significance; but they are of course female and male respectively. This is not explained.

In choosing between the two simultaneously published and equally available names, *leuschneri* and *rindgei*, I followed page priority in selecting *leuschneri* as the species name for the box-elder tussock moth. Unfortunately Riotte did the opposite and chose *rindgei* in his 1977 paper which I did not see before my own went to press.

The one oversight pointed out by Riotte that does cause me some embarrassment was my failure to interpret correctly the Latin word "degens" on the label pinned to the type of *O. detrita*. I should have recognized it.

Reference Cited

Riotte, J. C. E. 1971. Eine neue Art der Gattung *Orgyia* (Untergattung *Hemerocampa*) in Nordamerika (Lep.: Lymantriidae). *Entomologische Zeitschrift* 81(11): 105-115.

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Announcement

MONARCH BUTTERFLY CONSERVATION

After forty-one years of research, commencing in the summer of 1935, the overwintering site of the eastern population (east of the Rocky Mountains) in North America of the monarch butterfly, *Danaus plexippus plexippus,* was discovered in the Neovolcanic Plateau, a series of volcanic mountains sometimes referred to as the Great Cross Range, in southern Mexico. This unique phenomenon was first reported in the August, 1976 issue of the National Geographic Magazine - the field expedition responsible for the discovery being sponsored by the Committee on Research and Exploration of the National Geographic Society and the National Research Council of Canada.

Since countless millions of migrant monarch butterflies congregate each year in various locations (loci), ambiguously referred to as "sites" by some authors, covering the branches and trunks of over a thousand trees in one locus, the vulnerability of the butterflies became apparent to us. The roosting trees, consisting of various species of conifers, might be destroyed by fire, that which already posed a serious possibility on one occasion, or excess lumbering practices not to mention the hazards created by visitors intent on taking photographs.

The importance of protecting the overwintering monarchs in the various loci throughout the Mexican Site was brought to the attention of the Mexican authorities with special attention to the possibility of fire.

As a result of our working closely with the officials of Mexican television, Televisa de Mexico, this unique phenomenon was shown to the citizens of Mexico emphasizing the need for protecting the various loci where the monarchs congregated. The response to this appeal was most gratifying; hundreds of letters were received by the President of Televisa, Miguel Aleman, requesting protection for the monarch butterflies and suggesting that such areas be set aside as conservation areas.

As a result of meetings held with Dr. Ricardo Enriquez, Special Consultant to the Subsecretario Forestal y de La Fauna de Mexico, a law has now been passed declaring all areas between the levels of 2500 - 3500 m. of all mountains of the Neovolcanic Plateau as wildlife sanctuaries. These areas are now being patrolled by trained armed guards. A fine of $800.00 U.S. is imposed on anyone entering the protected areas without official sanction.

F. A. Urquhart & N. R. Urquhart: Scarborough College, University of Toronto, West Hill, Ontario M1A 1A4.

INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbrevations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

Illustrations: Color must be submitted as a transparency (i.e., slide) ONLY, the quality of which is critical. On request, the editor will supply separate detailed instructions for making the most suitable photographic ilustrations. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors **must** plan on illustrations for reduction to the 4 x 6½" page. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink at least twice the final size. Include a metric scale or calculate and state the actual magnification of each illustration as printed. Each figure should be cited and explained as such. The term "plate" should not be used. Each illustration should be identified as to author and title on the back, and should indicate whether the illustration be returned.

Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

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THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

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IN THIS ISSUE

Cover Illustration: *Uraba lugens,* last instar larva showing retention of head capsules of all prior instars. McFarland, pages 209-217.

THE JOURNAL
OF RESEARCH
ON THE LEPIDOPTERA

In Memoriam

Maculinea arion eutyphron

c 10,000 B.C.-1979 A.D.

the wide open spaces
are closing in quickly
from the weight
of the whole human race
Waylon Jennings

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Editorial

> *Things they are changing, the worlds rearranging,*
> *A time that will soon be no more*
>
> Waylon Jennings

Item: London, Sept. 22, 1979 (UPI): Scientists say the large Blue butterfly is extinct in England because the last known batch of eggs failed to hatch.

The large Blue became extinct in England in spite of a substantial effort to save the butterfly. According to Jeremy Thomas, who was in charge of the project for the Institute of Terrestrial Ecology, there were at least 30 colonies in the 1950s, which severely declined to four in the mid-sixties. These became extinct in 1967, 1971, 1975 and finally 1979. About half of the populations were expirated by direct cultural practice. Although organized efforts to save the Blue commenced nearly two decades before its loss, it was not until the Blue's complete requirements were defined that the early attempts were shown to be fruitless. By the time the requirements were known it was too late.

An important lesson of the loss was misplaced good intentions during the first stages of the conservation attempt. The preserves then set up were over-protected. By the time Thomas discovered that the key to maintenance of large Blue populations was one ant species, *Myrmica sabuleti*, a necessary high density of which required heavily grazed habitat (less than 2 cm turf), recovery in England was beyond hope. *Maculinea arion* in England was ironically loved to death. Thus, in future attempts to save threatened and endangered species the operational word is management. In turn, management demands good data. It should be mentioned that most populations of the five species of large Blues (*Maculinea*) throughout Europe are critically threatened, and a number of subspecies are already gone.

It has been predicted that in the coming decades extinctions will accelerate to a point where one million of some five to ten million extant plant and animal species will be erased by the year 2000. With them will go a treasury of germ plasms of incalcuable value to biological research, practical application and esthetics. Worldwide ecological stability may be simultaneously threatened.

Extinction is a natural process which with change, comprises the two sides of the coin of evolution. Extinction of a population results from environmental change to which the population is not fitted to cope,

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Attempted Mating Between Male Monarchs

In coastal California, on the sunny days of February and March, when the overwintering concentrations of Monarchs (*Danaus plexippus*) begin to disperse, numerous individuals may be seen in flight around the pine and cypress trees where they settle in Pacific Grove. It appears that the females often leave the area first, and the sex ratio is then strongly skewed to males. Numerous attempts at mating may be noted between males at this time. The picture shown here was taken late in February at Millar's Motel in Pacific Grove, which as an adjacent woodlot frequented by large numbers of Monarchs.

J. W. Tilden, 125 Cedar Lane, San Jose, California 95127

Editorial *continued*

including competition for the same niche with different kinds of organism. The spectrum of life forms we see today is the result of the interaction of change and extinction. From paleontological evidence the rates of both processes have not been constant, and at times spectacular, e.g., appearance of the vertebrate system and disappearance of the dinosaurs. The advent of acculturated man again accelerated the process, commencing in measurable ways during the past Pleistocene.

It is our position that responsible behavior demands an active stand to halt or circumvent massive inroads on ecosystems and further reduction in numbers of adaptive entities. We particularly urge the members of the Foundation to support activities such as the Xerces Society offers, emphasizing insect conservation, in addition to the more general environmental groups as World Wildlife Fund. Although there is no doubt that "development," by habitat modification, is quite beneficial to the human population immediately, the operation of limits, which must be imposed at *some* point, can only lead to the rational conclusion that further human population growth and "development" will start to depress the standard of life for all mankind in the very near future. We are currently formulating activities for the Lepidoptera Research Foundation to more directly participate in conservation efforts.

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The Butterfly Fauna of a Secondary Bush Locality in Nigeria

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and
Michael A. Cornes

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Introduction

When the senior author first visited Nigeria in 1967 he did not have a driving license and therefore needed to find a good collecting ground within easy striking distance of Lagos. In early June, 1967 the first visit was paid to the locality covered in this paper and it was then collected regularly for the next three months. All three authors visited the locality regularly in the months of May to September 1969. By then son many interesting species had turned up and so many species had been recorded that after the departure of the senior author in September, the two other authors visited the locality on roughly a monthly basis for the following three years. By conservative estimate more than 50 visits have been made with a total input of well over 300 manhours. Records were made for each month in which a given species was seen, but no attempt was made to record relative density, etc.

Nonetheless, our investigations of the locality must be one of the most comprehensive ever directed at secondary bush in West Africa. The total number of species recorded, 376, comprises about half of all the species known to occur in southwestern Nigeria and is about 80% of the total number recorded in Liberia. For these reasons alone we think it worthwhile to publish our results, but we also hope it will give a picture of the diversity and interest of the fauna which can persist even in severely disturbed environments in Africa. Considering that the remaining West African rainforests are fast disappearing (those of southwestern Nigeria, Gambari, Ilaro and Olokemeji are close to being destroyed despite their designation as forest reserves) it is encouraging to see that disturbed habitats manage to support such a rich fauna.

From time to time many of our friends or relatives have participated in collecting trips to the locality. Some have brought picnics and iced beer to tired researchers; many contributed to the collection; all were

Not Refereed

good company. *Abantis leucogaster* Mab. was first observed by Mr. Poul F. Larsen, whose description of this great rarity was greeted with disbelief till a specimen was finally caught the following week. We wish to thank all participants.

We also owe thanks to the local population which was friendly, helpful and never objected to our trespassing on their lands. On one occasion we narrowly avoided being drawn into serious discussion concerning the purchase of wives for unmarried members of the team. An old man brought a note of continuity into the project by describing an English collector who had been active in the area some 50 years earlier. This could only have been C.O. Farquharson, who was based at a nearby agricultural station and to whom we owe so much for his studies on the early stages of the Lycaenidae (Farquharson *et al.* 1922). We thought that our obvious persistence succeeded in transforming the local attitudes from puzzled amusement to grudging respect, but this may have been wishful thinking.

Description of the locality

Specimens from the locality in our collections are labelled 4 m. NW of Agege; Agege is a town immediately north of Lagos international airport. The locality itself is reached by taking the Agege Motor Road to a point seven kilometres north of the town where there is a prominent church on the left side of the main road. A dirt road on the left leads into the bush about 150 m past the church. One and a half kilometres along this dirt road is a crossroads. The area exploited in the survey lies a few kilometres to either side of the crossroads along the dirt road parallel to the Agege Motor Road.

Southern Nigeria is in the tropical rainforest zone and the original vegetation at Agege would have been tropical rainforest of the same nature as that in the Ilaro Forest Reserve some 50 km. further north. The original tree cover has long since disappeared, except for occasional traces, and has been replaced by plantations and agricultural land in fallow or in use. However, the intensity of agricultural exploitation is less than in most similar areas in the immediate vicinity of a large town. In some respects such an environment is ecologically more diverse than climax forest and this is undoubtedly a major factor in the richness of the fauna.

It is not possible to give a scientific description of the patchwork pattern of different habitats, but the following were prominent types:

Roads and open places: In many places the dirt road was bordered by a yellow composite which was a great favourite with many of the skippers, the Polyommatini, the Acraeidae and many Pierids and Nyphalids.

Many species caught on the flowers were never seen anywhere else. Species such as *Anthene* and *Eritis* used the road as a basking ground. It was also a major communication channel for the *Charaxes* which would often stop at suitable natural baits (four species were caught on a single fermenting oil-berry in half an hour).

Open fields: Open fields were usually planted with a mixture of cassava, maize and vegetables and were generally devoid of butterflies. Owing to similarity with savanna conditions, savanna invaders could sometimes be found here, especially apparently permanent populations of *Hamanumida daedalus* F.

Forest: In one place a small block of the original forest was partly conserved, as far as we could ascertain because it had magical ("juju") associations. Interesting and rare forest species still survived in this area, for example *Mimacraea darwini* Btl. It was also the foraging ground for driver ants, as we would often discover to our disadvantage since they prey on passing entomologists with gusto. It was always somewhat embarassing to have to rush out to the road, to strip down and then proceed to pick off hundreds of biting ants to the great amusement of passers-by.

Kola plantation: The plantations mainly consisted of mature trees which were poorly tended. The crowns were full of parasitic *Loranthus* and many of our *Iolaus*-grup records came from this habitat. Kola trees are very shady and the undergrowth was not dense, consisting often of large leaved gingers, on whose leaves the less sun-loving skippers liked to sit.

Cocoa plantation: In this habitat the shade trees were either old forest trees or kola, but sufficient sunshine penetrated to allow a richer undergrowth which would be indifferently cleared from time to time by the farmers. The butterfly fauna was quite rich and diverse, but somewhat unpredictable.

Mixed secondary shrub: These blocks consisted of fallow agricultural land in various stages of regeneration. Once the shrub reaches an age of about 10 years it becomes good and diverse hunting ground as the forest species start re-establishing themselves. More sun penetrates than in primary forest and in consequence a number of skippers and Satyrids are found which would otherwise not have been present. Some of the best "ant-trees" (see later) were in this type of habitat.

Swamp forest: A rivulet at the northern edge of the area was bordered by a mixture of swamp forest and palm shrubbery. The edge of this seemed to act as a communication channel from real forests further north (*Papilio hesperus* suddenly appeared here), but the swamp forest supported its own fauna of shade loving Nymphalidae and Satyridae, as well as some interesting colonies of *Epitola* and other Liptenini (infuriatingly out of reach). The palm shrubbery housed some of the large, scarce skippers (*Gamia, Gretna, Zophopetes*, etc.).

Ant trees: Special mention must be made of trees carrying the bee-hive shaped nests of Crematogasterine ants, which were dotted throughout the different habitats. Many of the most interesting Lycaenidae (Lipteninae) are associated with such trees where they feed on lichens on the tree trunk. Some species were virtually limited to a single tree. In one place we could be certain to pick up one or two *Micropentila dorothea* B.B.; *Pseuderesia eleaza* Hew. had one vantage point which was occupied time and time again by different specimens. Near ant nests it was often possible to find five or six individuals of three or four species sitting on a single dry twig.

Analysis of the fauna

As shown in table 1, we caught a total of 376 species during the six years of research. This constitutes about half the total known from southwestern Nigeria. It is as many as were recorded from Gambari Forest Reserve by Riley & Cornes (1970, 1971, 1972) during a similar survey from 1960 to 1969, though the Gambari records are not quite as comprehensive. It is about 80% of the species known to occur in Liberia (Fox, Lindsey, Clench & Miller 1965). Although we knew the area to be rich, none of us would have guessed at the outset that the total would rise to such a level.

Table 1

Breakdown by families of the butterflies known from Agege, Gambari Forest Reserve and Liberia

FAMILY	AGEGE		GAMBARI		LIBERIA	
	No.	%	No.	%	No.	%
Papilionidae	13	3.4	14	3.7	18	3.8
Pieridae	20	5.3	25	6.6	22	4.6
Danaidae	6	1.6	6	1.6	5	1.1
Satyridae	22	5.9	19	5.0	27	5.7
Charaxinae	16	4.3	29	7.7	17	3.6
Nymphalinae	77	20.6	95	24.9	110	23.2
Acraeinae	19	5.1	22	5.8	28	5.9
Libytheidae	1	—	1	—	1	—
Lycaenidae	115	30.7	95	24.9	138	29.1
Hesperiidae	87	23.1	75	19.8	109	22.9
Total	376	100	381	100	475	100

A glance at the table will show that compared to the Gambari list, the Nymphalinae and especially the Charaxinae at Agege are under-represented. This is because many of these species genuinely appear to be restricted to primary forest. The Hesperiidae, on the other hand, are over-represented in the Agege sample. We think this is due to the fact that the Hesperiidae prefer disturbed habitats to primary forest, though this is not universally true. The over-representation of Lycaenidae in the Agege sample is probably largely due to the fact that species were more easily collected in the disturbed habitat, while in a primary forest many of the scarcer species never descend from the canopy. The fact that we caught more species of Satyridae at Agege than in Gambari is probably not due to chance; they are all grass feeders and grass is not plentiful in climax forest. In Liberia Fox collected in all types of habitat and it is interesting to see that the percentage breakdown of the Liberian list matches that of Agege almost perfectly.

As shown in Table 2, the degree of overlap between the species collected in Gambari and at Agege is almost two thirds. The total number of species in these two selected localities is almost as high as the total recorded for Liberia.

Table 2

Degree of overlap in species caught in Gambari Forest Reserve and at Agege

Locality	Number Caught	Percent
Agege only	**87**	**18.6**
Gambari only	**92**	**19.7**
Both localities	**289**	**61.7**
Total	**468**	**100**

The majority of the species caught at Agege are typical representatives of the rainforest fauna with a small element of ubiquitous species. All of these may be found also in the rainforest itself. The more open conditions do allow for some penetration of savanna elements which are unlikely to occur in primary forest. The savanna species are listed in table 3.

Table 3

Savanna species penetrating into the Agege locality

Graphium pylades
Graphium leonidas
Colotis evippe *
Eurema brigitta
Melanitis leda *
Danaus chrysippus
Hamanumida daedalus
Neptis morosa
Precis oenone *
Precis chorimene
Precis octavia
Phalanta phalanta
Lipaphnaeus leonina
Syntarucus babaulti
Syntarucus pirithous
Pseudonacaduba sichela
Lepidochrysops quassi *
Euchrysops malathana
Eicochrysops hippocrates
Zizeeria knysna *
Spialia ploetzi *
Spialia spio
Spialia diomus
Gomalia elma
Fresna netopha *
Fresna cojo
Fresna nyassae
Borbo perobscura
Borbo fanta

* Species of savanna origin which have managed to adapt almost totally to forest conditions.

The savanna element comprises 30 species, 8 percent of the total. This is a relatively low number, compared for example to the fauna of the coastal strip and Ikoyi Island, and it may indicate that savanna species find penetration of the forest zone very difficult indeed.

Seasonal distribution

Southwestern Nigeria has a fairly pronounced dry season from November/December to February/March, though rainfall is never totally absent in any month. We were therefore interested in studying the effect of seasonality on the fauna. Data are given in table 4 below.

Table 4

Number of species caught by family and month

FAMILY	MONTH OF CAPTURE											
	1	2	3	4	5	6	7	8	9	10	11	12
Papilionidae	7	8	7	10	7	5	4	7	7	3	8	6
Pieridae	12	9	6	6	12	10	8	14	8	10	8	12
Danaidae	3	4	2	2	1	1	1	3	2	4	4	3
Satyridae	10	9	5	9	11	10	13	16	6	8	7	10
Charaxinae	3	4	4	4	6	4	9	4	3	5	3	3
Nymphalinae	35	33	31	32	39	30	40	43	28	37	40	39
Acraeinae	9	7	4	1	6	1	3	7	6	8	11	14

Lycaenidae	44	56	47	51	47	49	38	45	33	43	65	51
Hesperiidae	18	20	20	17	35	32	47	50	33	33	31	27
TOTAL (376)	**141**	**150**	**126**	**132**	**164**	**142**	**163**	**189**	**126**	**151**	**177**	**165**
Percent of total	**38%**	**40%**	**34%**	**35%**	**44%**	**38%**	**44%**	**50%**	**34%**	**40%**	**47%**	**44%**

Although we made records of all species on a monthly basis, some extra problems occur in the monthly breakdown. We were able to identify most species on the wing, but in certain genera it is necessary to catch a specimen to be certain of its identity. This is true of the *Bicyclus,* the *Neptis,* certain skippers and above all blues from the *Epitola* and *Iolaus*-groups. Some of these are unfortunately also amongst the most elusive. The monthly totals are therefore clear underestimates, but the level of underestimation is probably the same from month to month. The table indicates that as far as the number of species is concerned, there are no significant peaks or troughs. The number of individuals on the wing is higher during the wet season. The savanna species, the Acraeidae and species such as *Graphium antheus* Cr. and *Lepidochrysops nigeriae* Stempffer are clearly most prominent during the dry season. The larger forest Nymphalidae *(Charaxes, Euphaedra, Euriphene* and *Bebearia)* prefer the wet season. Certainly seasonal patterns are less than might have been a priori expected.

The lack of defined seasonality does not mean that generational patterns could not be observed. For certain groups they were so pronounced as to provide the antidote to the boredom which would otherwise be involved in revisiting the same restricted locality so often. Every so often, after an absense of a fortnight we would find a new dominant group on the wing; a sudden preponderance of Pierids; mass eclosion of a few skippers we had rarely seen before; half a dozen *Acraea* which we had not seen for months. Quite often a species which we had never seen before would be present in some quantity. There is no doubt that part of the reason for this lies in the fact that there is significant displacement of species, even though we never say any active migrations. Accordingly, it might be expected that continued surveillance of the locality will continue to yield more species. It is quite likely, on the other hand, that some of the rarer ones we found may not turn up again.

Rarity

It is of some interest to list the species which we turned up on only one or two occasions during the research period, since such information will assist in assessing the degree to which species are resident and the degree of random displacement. A list of these rarities is given in table 5.

Table 5

Species which were noted only once or twice during the 1967-73 period

Papilio cynorta
Papilio hesperus
Hallelesis asochis
Euxanthe eurinome
Charaxes etisipe
Euptera elabontas
Euphaedra eleus
Neptis nysiades
Neptis puella
Neptis strigata
Precis octavia
Acraea jodutta
Liptena septistrigata
Liptena similis
Liptena rochei
Eresina saundersi
Aslauga lamborni
Epitola crowleyi
Epitola gordoni
epitola gerina
Epitola elissa
Epitola sublustris
Pilodeudorix camerona
Diopetes deritas
Virachola diomedes
Iolaphilus iulus
Iolaphilus panaperata
Aphnaeus orcas
Liaphnaeus leonina
Anthene crawshayi
Neurypexina lyzianus
Triclema lucretilis
Triclema obscura
Gorgyra heterochrus
Gorgyra diversata
Pardaleodes tibullus
Semalea pulvina
Hypoleucis tripunctata
Gamia buchholzi
Gamia shelleyi
Gretna waga
Platylesches picanini
Borbo fanta
Borbo perobscura
Borbo micans

The list of real rarities comprises 45 species, or about 12 percent of the total. A scrutiny of table 5 will show that the majority are genuinely uncommon species which one would be extremely happy to capture anywhere (e.g. *E. elabontas, N. strigata, N. puella, E. saundersi,* most of the *Epitola, P. camerona, D. deritas, A. orcas, L. leonina* and to a lesser extent some of the skippers). Some are obvious strays from primary forest (e.g. *P. hesperus, H. asochis, E. eleus* and *A. jodutta).* A few species are savanna invaders (e.g. *B. fanta, B. perobscura* and possibly *L. leonina,* though this is generally very rare). It would thus seem that the overwhelming majority of the 376 species in question are at least temporary residents of the locality.

Conversely it is worthwhile to consider briefly the most common species found in the locality. In fact, there were relatively few which were almost certainly present at any visit at any time of the year. These are listed in Table 6.

Table 6

Species present at almost all visits paid to the locality

Papilio dardanus	*Precis sophia*
Papilio demodocus	*Precis terea*
Appias sylvia	*Precis oenone*
Belenois calypso	*Hypolimnas salmacis*
Leptosia hybrida	*Mimeresia libentina*
Colotis evippe	*Citrinophila marginalis*
Eurema hecabe	*Oxylides faunas*
Bicyclus dorothea	*Thermoniphas micylus*
Ypthima doleta	*Tagiades flesus*
Bebearia theognis	*Pardaleodes edipus*
Euphaedra medon	*Pteroteinon caenire*
Pseudoneptis ianthe	
Neptis melicerta	
Ariadne enotrea	

Only 25 species, or about 6.6 percent of the total are included in the group of most common species. Probably another 15 species also belong to the group. An evaluation of the relative frequency of the species may be supplemented by a listing of all species according to the number of months in which records were made. The data are summarized in table 7.

Table 7

Number of months in which each species was recorded during the period of investigation

Months	Number	Percent
11-12 months	47	12.5
9-10 months	32	8.5
7- 8 months	39	10.4
5- 6 months	43	11.4
3- 4 months	77	20.5
1- 2 months	138	36.7
Total	**376**	**100**

Conclusion

In retrospect we regret that we did not maintain a detailed diary of observations, but at the time we were involved in the cataloguing of the Nigerian Rhopalocera as a whole. After Larsen's departure, Riley and Cornes started work on the Diptera and Heterocera (Cornes 1969, 1971; Cornes, Riley & St. Leger no date; Riley 1971 a & b). Nevertheless, the primary objectives of the investigation were achieved.

In February 1978 Larsen and Riley had the opportunity of revisiting the locality for half an hour and it is a pleasure to be able to report that it has survived beautifully the environmental degradation which is going on apace in southwestern Nigeria. We observed more than 50 species of butterfly, including one species not on the list, *Asterope occidentalium* Mab.

The richness of the fauna in this locality may have implications for conservation strategies. Most forests in Nigeria, Benin, Togo and Ghana seem destined to disappear in the foreseeable future, despite their classification as forest reserves. It therefore becomes important, and probably more manageable, to conserve areas with a mixture of plantations and shifting agriculture with long fallow periods. Attention must also be paid to the juju woods which are threatened as the modernisation process breaks down traditional taboos. If an interlocking network of such areas remains, then a significant proporition of the insect fauna will survive the destruction of primary forest. Whether this will happen is far from certain; large stretches of land between Accra and Kumasi in Ghana have been converted to cassava monoculture in the course of just six years. Mobilisation of the combination of political will and administrative skill to implement a conservation strategy in West African countries is going to be a very difficult task. For this reason alone, faunal surveys such as the present paper are urgently needed before these resources are irrevocibly destroyed.

Systematic list and monthly records

FAMILY AND SPECIES	MONTH											
	1	2	3	4	5	6	7	8	9	10	11	12
PAPILIONIDAE												
Papilio dardanus Brown	X	X	X	X	X	X	X	X	X	X	X	X
Papilio cynorta F.				X								
Papilio zenobius Gt.	X	X	X	X	X	X	X	X	X		X	X
Papilio hesperus West			X									
Papilio sosia R. & J.		X						X				
Papilio nireus L.	X	X			X				X		X	X
Papilio bromius Dbl.	X			X	X	X					X	
Papilio demodocus Esp.	X	X	X	X	X	X	X	X	X		X	X
Papilio menestheus Drury	X	X	X	X	X		X	X	X	X	X	X
Graphium pylades F.				X								
Graphium leonidas F.		X		X				X	X		X	
Graphium antheus Cr.		X	X	X		X						
Graphium policenes Cr.	X	X	X	X	X			X	X	X	X	X
PIERIDAE												
Appias sylvia F.	X	X	X	X	X	X	X	X	X	X	X	X
Appias sabina Fld.						X						
Appias epaphia Cr.									X	X		
Belenois calypso Dr.	X	X	X	X	X	X	X	X	X	X	X	X
Belenois theora Dbl.	X											X
Mylothris chloris F.	X	X	X					X		X		X
Mylothris rhodope F.*	X				X			X			X	X
Leptosia marginea Mab.		X				X	X	X	X			
Leptosia medusa Cr.					X			X				
Leptosia alcesta Cr.	X	X			X	X	X	X	X	X	X	X
Leptosia hybrida Bern.	X	X	X	X	X	X	X	X	X	X	X	X
Colotis evippe L.	X	X	X	X	X	X	X	X		X	X	X
Nepheronia thalassina Bdv.					X	X		X	X			
Nepheronia argia F.								X				
Nepheronia pharis Bdv.								X				
Catopsilia florella F.	X			X	X	X	X	X		X	X	X
Eurema brenda Dbl.	X							X				X
Eurema brigitta Cr.	X	X			X							X
Eurema hapale Mab.									X	X		
Eurema hecabe L.	X	X	X	X	X	X	X	X	X	X	X	X
DANAIDAE												
Danaus chrysippus L.	X	X	X	X						X	X	X
Danaus limniace Cr.											X	
Amauris tartarea Mab.		X	X									
Amauris hecate Btl.								X		X		
Amauris niavius L.	X	X			X			X	X	X	X	X
Amauris hyalites Btl.	X	X		X		X	X	X	X	X	X	X

FAMILY AND SPECIES	MONTH											
	1	2	3	4	5	6	7	8	9	10	11	12
SATYRIDAE												
Elymnias phegea F.	X				X	X				X		
Elymnias bamakoo West.	X	X	X	X	X	X	X	X			X	X
Melanitis leda Dr.		X										X
Melanitis parmeno Dbl.	X	X						X				X
Melanitis chelys F.								X				
Bicyclus italus Hew.							X	X				
Bicyclus xeneas Hew.					X		X	X		X		
Bicyclus taenias Hew.							X	X				
Bicyclus ignobilis Btl.	X	X			X		X	X		X	X	X
Bicyclus evadne Stgr.		X				X						
Bicyclus madetes Hew.	X		X		X	X	X	X	X	X	X	X
Bicyclus mandanes Hew.								X				
Bicyclus auricruda Btl.							X					
Bicyclus sandace Hew.						X	X	X				
Bicyclus technatis Hew.						X	X	X	X			
Bicyclus uniformis B.B.	X	X										X
Bicyclus dorothea Cr.	X	X		X	X	X	X	X	X	X	X	X
Bicyclus vulgaris Btl.	X	X	X		X	X	X	X	X	X	X	X
Bicyclus funebris Guen.					X			X				
Bicyclus sanaos Hew.	X	X	X	X	X	X	X	X	X	X	X	X
Hallelesis asochis Hew.					X							
Ypthima doleta Kby.	X	X	X	X	X	X	X	X	X	X	X	X
NYMPHALIDAE												
Charaxinae												
Euxanthe eurinome Cr.							X					
Stonehamia varanes Cr.			X		X		X	X				
Stonehamia fulvescens Aur.	X					X	X			X	X	
Charaxes protoclea Feist.				X		X				X		
Charaxes boueti Feist.	X							X				X
Charaxes cynthia Btl.							X			X	X	
Charaxes lucretius Cr.		X	X	X	X		X					
Charaxes castor Cr.							X					
Charaxes brutus Cr.			X									
Charaxes numenes Hew.									X			
Charaxes tiridates Cr.		X		X	X	X		X	X	X	X	
Charaxes eupale Drury	X				X		X	X	X		X	X
Charaxes etisipe Gt.			X									
Charaxes anticlea Drury					X		X			X		
Charaxes etheocles Cr.						X						
Charaxes laodice Drury		X		X	X		X					

FAMILY AND SPECIES	MONTH											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Nymphalinae												
Cymothoe egesta Cr.				X								
Cymothoe caenis Drury						X	X					
Cymothoe coccinata Hew.				X	X		X					
Euptera elabontas Hew.							X					
Euryphura chalcis Feld.			X		X							
Euryphura plautilla Hew.					X	X	X	X				
Euriphene tadema Hew.		X					X		X	X	X	X
Euriphene barombina Aur.								X				
Euriphene doriclea Drury							X					
Euriphene ampedusa Hew.											X	
Euriphene atossa Hew.								X	X			
Bebearia tentyris Hew.	X				X		X	X				X
Bebearia absolon F.					X		X	X			X	
Bebearia zonora Btl.					X	X		X	X			
Bebearia mandinga Fld.							X	X				
Bebearia oxione Hew.						X	X	X				
Bebearia mardania F.					X	X				X		
Bebearia theognis Hew.	X	X	X	X	X	X	X	X	X	X	X	X
Bebearia plistonax Hew.			X		X	X	X	X		X		
Euphaedra wardi Druce	X	X		X	X		X	X		X	X	
Euphaedra harpalyce Cr.	X	X	X	X	X	X	X	X		X	X	X
Euphaedra medon L.	X	X	X	X	X	X	X	X	X	X	X	X
Euphaedra xypete Hew.					X					X	X	
Euphaedra themis Hub.	X	X				X	X	X	X	X	X	X
Euphaedra janetta Btl.	X	X	X	X	X	X	X	X	X	X	X	X
Euphaedra ceres F.	X	X			X		X		X	X	X	X
Euphaedra edwardsi Hoev.	X									X		
Euphaedra ruspina Hew.					X			X				
Euphaedra eleus Drury							X					
Hamanumida daedalus F.		X	X	X		X					X	X
Aterica galene F.	X	X			X	X	X	X	X	X	X	X
Cynandra opis Drury	X				X		X	X	X	X	X	X
Catuna oberthueri Karsch	X		X	X				X				
Catuna crithea Drury		X						X	X	X	X	X
Catuna angustata Fld.	X							X		X	X	X
Pseudoneptis ianthe Cr.	X	X	X	X	X	X	X	X	X	X	X	X
Pseudacraea semire Cr.	X	X	X	X	X	X	X	X	X	X	X	X
Pseudacraea warburgi Aur.		X		X		X	X	X		X	X	
Pseudacraea eurytus L.					X							
Pseudacraea striata Btl.			X					X				
Pseudacraea lucretia Cr.	X				X	X	X			X		X

FAMILY AND SPECIES	MONTH											
	1	2	3	4	5	6	7	8	9	10	11	12
Neptis nemetes Hew.	X	X	X			X		X		X		X
Neptis morosa Over.*		X										X
Neptis nysiades Hew.			X					X				
Neptis puella Aur.											X	
Neptis nicomedes Hew.					X							
Neptis strigata Aur.			X									
Neptis paula Stgr.	X	X	X								X	X
Neptis nicoteles Hew.					X						X	
Neptis nicobule Holl.	X				X							
Neptis nebrodes Hew.		X	X	X				X	X		X	X
Neptis intermedia Sch.				X			X	X				
Neptis melicerta Drury*	X	X	X	X	X	X	X	X	X	X	X	X
Cyrestis camillus F.		X	X	X	X		X	X			X	
Byblia acheloia Wall.	X			X					X			X
Mesoxanthe ethosea Drury	X				X							
Ariadne enotrea Cr.	X	X	X	X	X	X	X	X	X	X	X	X
Eurytela hiarbas Drury	X	X	X	X	X	X		X	X	X	X	X
Eurytela dryope Cr.						X						
Kallima rumia Dbl.	X	X		X	X	X	X	X	X	X	X	X
Kallima cymodoce Cr.			X	X			X	X	X	X	X	
Salamis cacta F.	X											
Hypolimnas salmacis Drury		X	X	X	X	X	X	X	X	X	X	
Hypolimnas misippus L.	X	X	X						X	X	X	X
Hypolimnas dinarcha Hew.				X	X							
Hypolimnas dubius de B.	X	X		X	X	X	X	X	X	X	X	X
Precis chorimene Guerin			X									X
Precis stygia Aur.	X	X	X	X	X	X	X	X	X	X	X	X
Precis terea Drury	X	X	X	X	X	X	X	X	X	X	X	X
Precis pelarga F.	X	X	X	X						X	X	X
Precis ocavia Cr.												X
Precis sophia F.	X	X	X	X	X	X	X	X	X	X	X	X
Precis oenone L.	X	X	X	X	X	X	X	X	X	X	X	X
Antanartia delius Drury				X			X	X	X	X	X	X
Phalanta eurytis Drury	X	X	X	X	X		X		X	X	X	X
Phalanta phalanta Drury						X	X					
ACRAEINAE												
Bematistes vestalis Fld.									X		X	
Bematistes alcinoe Fld.											X	
Bematistes umbra Drury										X		X
Bematistes consanguinea Aur.											X	X
Bematistes epaea Cr.	X	X	X		X			X	X	X	X	X

FAMILY AND SPECIES	MONTH											
	1	2	3	4	5	6	7	8	9	10	11	12
Acraea quirina F.	X	X	X		X						X	X
Acraea admatha Hew.	X	X			X		X	X		X		X
Acraea zetes L.	X	X		X	X	X			X	X	X	
Acraea egina Cr.	X		X					X				X
Acraea lycia F.	X				X			X				X
Acraea bonasia F.		X						X	X	X	X	X
Acraea oberthueri Btl.	X	X										X
Acraea peneleos W.							X	X	X	X		
Acraea parrhasia F.							X					X
Acraea eponina Cr.			X					X	X	X	X	X
Acraea orestia Hew.										X		X
Acraea alciope Hew.	X									X	X	
Acraea jodutta F.											X	
Acraea lycoa Gt.	X	X			X						X	X
LIBYTHEIDAE												
Libythea labdaca W.		X		X	X			X		X	X	X
LYCAENIDAE												
Telipna acraea Dbl. & Hew.	X	X				X	X	X				
Telipna rothi G.-S.	X						X	X	X		X	X
Ptelina carnuta Hew.	X	X		X	X	X	X			X	X	X
Pentila petreia Hew.				X			X	X			X	
Pentila nigeriana St. & Ben.					X				X			
Pentila abraxas Dbl. & Hew.					X		X	X		X	X	
Mimacraea darwini Btl.	X				X		X		X	X	X	X
Mimeresia libentina He.	X	X	X	X	X	X	X	X	X	X	X	X
Pseuderesia eleaza Hew.	X		X	X	X	X	X	X			X	
Eresiomera isca Hew.	X	X		X	X	X		X	X	X	X	X
Citrinophila erastus Hew.		X	X	X	X	X				X	X	X
Citrinophila marginalis Ky.	X	X	X	X	X	X	X	X	X	X	X	X
Larinopoda aspidos H.H. Dr.	X	X	X		X	X	X	X	X	X	X	X
Falcuna gitte Bennet	X											X
Liptena submacula Lathy	X	X	X	X	X	X	X	X		X	X	X
Liptena allaudi Mab.*						X		X				
Liptena august Suff.*			X	X						X		
Liptena septistrigata B.B.	X											
Liptena flavicans S.&K.	X	X	X	X	X	X	X	X	X	X	X	X
Liptena similis Ky.							X					
Liptena rochei Stempf.												
Liptena otlauga S.&K.		X	X	X							X	X
Tetrarhanis simplex Aur.	X	X	X		X	X	X	X	X	X	X	X
Tetrarhanis stempfferi Ber.	X	X		X		X	X			X	X	X

FAMILY AND SPECIES	**MONTH**											
	1	2	3	4	5	6	7	8	9	10	11	12
Micropentila dorothea B.B.	X	X		X		X	X	X	X	X	X	X
Eresina saundersi Stempf.					X							
Eresina pseudofusca Stempf.			X	X								
Aslauga lamborni B.B.										X		
Aslauga vininga Hew.	X	X			X			X		X	X	X
Euliphyra leucyanea Hew.			X		X							
Neaveia lamborni H.H. Druce								X				
Epitolina dispar Ky.	X	X	X	X	X	X	X	X		X	X	X
Epitolina catori B.B	X	X	X	X	X	X			X	X	X	X
Epitola posthumus F.		X	X	X		X	X	X	X	X	X	X
Epitola crowleyi Sharpe								X				
Epitola katherinae Poul.		X								X	X	X
Epitola gordoni H.H. Druce											X	
Epitola gerina Hew.									X			
Epitola elissa S.									X			
Epitola ikoya Roche		X	X	X	X			X	X	X	X	
Epitola congoana Aur.	X	X	X	X	X	X	X	X	X	X	X	X
Epitola carcina Hew.											X	X
Epitola sublustris Btl.						X						
Phytala hyettoides Aur.			X								X	X
Phytala henleyi Ky.					X						X	X
Aethiopana honorius F.	X		X	X	X			X	X	X		
Hewitsonia boisduvali Hew.							X		X		X	X
Hewitsonia similis Aur	X		X	X		X				X		
Megalopalpus metaleucus K.					X							
Megalopalpus zymna West.					X			X				X
Lachnocnema brimo Karsch	X		X	X	X		X	X		X	X	
Hypokopelates viridis Stf.	X	X	X			X				X		
Pilodeudorix camerona Pl.								X				
Diopetes deritas Hew.											X	
Deudorix odana H.H. Druce						X		X			X	
Deudorix lorisona Hew.			X			X	X					
Deudorix diomedes Jack.		X										
Oxylides faunas Drury	X	X	X	X		X	X	X	X	X	X	X
Hypolycaena hatita Hew.		X				X	X				X	
Hypolycaena nigra Btl.	X			X								
Hypolycaena antifaunus West.	X	X	X		X	X		X			X	
Hypolycaena lebona Hew.	X	X	X			X		X	X	X	X	X
Hypolycaena dubia Aur.		X	X	X								
Hypolycaena philippus F.		X	X	X	X	X						
Dapidodigma hymen F.	X	X	X	X	X	X			X	X	X	X
Taneutheria timon F.	X	X	X	X	X	X		X		X	X	X
Philiolaus parasilanus Rebel		X								X	X	X
Iolaphilus alcibiades Ky.				X				X				

FAMILY AND SPECIES	MONTH											
	1	2	3	4	5	6	7	8	9	10	11	12
Iolaphilus julus Hew.		X										
Iolaphilus paneperata H.H. Dr.											X	
Epamera iasis Hew.	X					X				X		
Epamera maesa Hew.			X			X						
Epamera laon Hew.	X	X				X						
Epamera bellina Plotz		X			X				X	X	X	
Epamera sapphirinus Aur.		X		X		X				X		
Epamera aethria Karsch		X					X			X	X	
Iolaus eurisus Cr.		X	X	X		X	X					
Aphnaeus orcas Drury			X									
Spindasis menelas H.H. Druce					X	X						
Lipaphnaeus leonina Sh.		X										
Axiocerces harpax F.		X	X			X						
Spalgis lemolea H.H. Druce					X							
Anthene rubricincta Holl			X									
Anthene liodes Hew.				X		X	X					
Anthene lunulata Tr.			X	X	X	X						
Anthene sylvanus Drury	X	X	X	X	X	X		X	X	X	X	X
Anthene larydas Cr.	X	X	X	X	X	X				X	X	X
Anthene crawshayi Btl.			X									
Anthene lachares Hew.	X	X										X
Anthene locuples GS.						X	X	X		X		
Anthene flavomaculatus S.&K.			X	X	X	X						
Neurypexina lyzianus Hew.											X	
Triclema lamias Hew.								X			X	
Triclema lucretilis Hew.												X
Triclema lacides Hew.	X	X						X				
Triclema obscura H.H. Druce												X
Phlyaria cyara Hew.				X	X	X	X	X	X		X	
Uranothauma falkensteini Btl.		X										
Cacyreus lingeus Cr.								X		X	X	X
Cacyreus audeoudi Stempf.				X	X	X	X	X	X	X	X	X
Castalius carana Hew.				X	X		X	X	X	X	X	
Syntarucus babaulti Stempf.	X	X	X	X								
Syntarucus pirithous L.	X	X	X	X								
Azanus isis Drury			X	X						X		
Azanus mirza Plotz	X		X	X							X	X
Pseudonacaduba sichela Wlk.	X			X			X				X	
Lepidochrysops quassi Karsch							X	X	X		X	
Lepidochrysops nigeriae St.	X	X	X	X	X						X	X
Euchrysops malathana Bdv.	X	X						X	X			
Eicochrysops hippocrates F.	X	X	X	X	X	X		X	X	X	X	X

FAMILY AND SPECIES	MONTH											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Thermoniphas micylus Cr.	X	X	X	X	X	X	X	X	X	X	X	X
Oboronia punctatus Dew.	X	X	X	X	X		X	X	X	X	X	X
Athysonata ornata Mab.	X		X	X	X	X	X	X	X	X	X	X
Zizeeria knysna Trim.	X	X			X		X				X	X
Zizula hylax F.	X	X	X	X	X	X				X	X	X
HESPERIIDAE												
Coeliades chalybe West.	X	X			X	X	X	X			X	X
Coeliades libeon Dr.						X						
Coeliades forestan Cr.					X		X	X	X			X
Coeliades hanno Plotz							X	X	X			
Celaenorrhinus proxima Mab.	X				X	X	X	X	X	X	X	X
Celaenorrhinus galenus F.		X			X		X	X	X	X	X	
Celaenorrhinus medetrina Hew.												
Celaenorrhinus boadicea Mab.									X		X	
Tagiades flesus F.	X	X	X	X	X	X	X	X	X	X	X	X
Eagris denuba Plotz								X				
Eagris hereus Dr.	X	X				X	X	X	X	X	X	X
Eagris tetrastigma Mab.							X					X
Procamptra rara Holl.	X	X	X	X	X	X	X	X		X	X	X
Eritis melania Mab.	X		X		X	X		X		X		X
Sarangesa tertullianus F.							X	X	X		X	
Sarangesa thecla Plotz			X	X	X	X	X	X	X	X	X	
Abantis leucogaster Mag.	X	X					X	X	X	X		
Spialia ploetzi Aur.		X	X	X	X	X	X		X	X	X	X
Spialia diomus Hopf.			X					X				
Spialia spio L.					X			X				
Gomalia elma Trim.			X					X				
Prosopalpus styla Ev.					X	X		X				
Gorgyra aretina Hew.					X	X	X	X	X	X		X
Gorgyra heterochrus Mab.					X							
Gorgyra subnotata Holl.				X								
Gorgyra moquerysii Holl.					X					X		
Gorgyra minima Holl.					X							
Gorgyra sara Ev.			X				X	X	X		X	
Gorgyra diversata Holl.					X							
Gorgyra subfacatus Mab.							X	X			X	
Gorgya pali Ev.				X				X				
Ceratrichia phocion F.											X	
Ceratrichia semilutea Mab.						X						
Pardaleodes incerta Snel.	X	X										
Pardaleodes edipus Cr.	X	X	X	X	X	X	X	X	X	X	X	X

FAMILY AND SPECIES	**MONTH**											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Pardaleodes sator West				X			X	X	X	X		
Pardaleodes tibullus F.		X										
Xanthodisca vibius Hew.										X	X	X
Xanthodisca astrape Holl	X	X			X	X		X		X		
Rhabdomantis galatia Hew.			X					X			X	
Rhabdomantis sosia Mab.			X	X	X	X	X	X	X	X		X
Osmodes lux Holl.							X	X				
Osmodes thora Plotz			X		X	X	X	X	X	X	X	
Osmodes costatus Aur.		X						X				
Osphantes ogawena Mab.					X	X						X
Acleros placidus Plotz		X			X	X	X	X	X	X	X	X
Acleros mackeni Trim.					X	X	X	X				
Acleros ploetzi Mab.	X	X				X	X	X	X			X
Acleros nigrapex Stgr.									X	X		X
Semalea pulvina Plotz											X	
Hypoleucis tripunctata Mab.			X									
Hypoleucis ophiusa Hew.	X	X	X	X	X	X	X	X				
Meza meza Hew.	X		X			X	X	X	X	X	X	X
Meza elba Ev.					X	X		X				
Meza cybeutes Holl.							X	X	X	X	X	
Andronymus neander Plotz							X					
Andronymus caesar F.							X	X			X	
Andronymus hero Ev.							X			X		
Andronymus helles Ev.							X					
Andronymus evander Mab.					X		X	X	X			X
Zophopetes ganda Ev								X				
Zophopetes cerymica Hew.						X	X		X			
Gamia buchholzi Plotz					X							
Gamia shelleyi Sharpe												
Gamia shelleyi Sharpe							X					
Gretna waga Plotz							X					
Gretna cylinda Hew.			X				X				X	X
Pteroteinon laufella Hew.	X			X	X	X	X	X	X	X	X	X
Pteroteinon caenira Hew.	X	X	X	X	X	X	X	X	X	X	X	X
Pteroteinon pruna Ev.					X	X		X				
Caenides dacela Hew	X	X	X	X	X	X	X	X	X	X	X	X
Caenides kangvensis Holl.					X	X		X		X		
Caeides dacena Hew.								X			X	
Monza cretacea Snel.									X			X
Monza alberti Holl.			X		X		X	X	X	X		
Melphina unistriga Holl.			X	X		X		X		X		X
Melphina statirides Holl.				X		X			X	X	X	
Fresna netopha Hew.	X	X	X	X	X		X	X	X	X	X	

FAMILY AND SPECIES	MONTH											
	1	2	3	4	5	6	7	8	9	10	11	12
Fresna nyassae Hew.							X					
Fresna cojo Karsch											X	X
Platylesches picanini Holl.							X					
Baoris fatuellus Hopf.	X	X			X	X	X	X		X		X
Pelopidas thrax Hub.					X		X	X	X		X	
Borbo fanta Ev.							X					
Borbo perobscura H.H. Druce												X
Borbo micans Holl.								X				
Borbo gemella Mab.						X	X	X				

*Observations may cover more than one taxon.

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The Rhopalocera of Santa Cruz Island, California[1]

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Abstract.—Surveys of Santa Cruz Island in April, May and June of 1966 recorded 27 species of butterflies. Records from other surveys add another 6, for a total of 33 species. This is less than half the number that would be found in comparable habitats on the adjacent mainland at the same times of year. Only one endemic subspecies was found, all others being well documented on the mainland. Several species were present in much greater numbers than usually noted in coastal California, probably due to lack of competition. Other species of ubiquitous or very common occurrence on the mainland were not found at all on the island. This correlates with other offshore islands having vrying degrees of faunal reduction, often depending upon their isolation from continental land masses. In addition, the *native* flora and fauna on S.C.I. may be due to the abundance of domestic and feral animals, combined with the introduction of European-type weeds.

Introduction

Santa Cruz Island, Santa Barbara County, California, was surveyed for insects of all Orders from 25 April to 2 May 1966 and again from 7 to 10 June 1966, by the California Insect Survey, University of California, Berkeley. The April-May trip included Jerry A. Powell, Paul Rude, Joe Wolf and RLL. The June trip consisted of only JAP and RLL. In addition, this paper includes records from surveys by Charles L. Remington (CR); Paul A. Opler and Jerry A. Powell (O & P), 14-16 March 1969; David B. Weissman (DW), 1 Aug. 1969; and Glenn A. Gorelick (GG), 23-30 June 1978. Scott E. Miller, Santa Barbara Museum of Natural History, contributed data from his island research.

The overall program of the 1966 surveys was to sample all Insecta and some related arthropods on the island. The Lepidoptera herein treated represent only one phase of the total survey. Since many of the species are closely associated with certain hosts and particular habitats, these situations were sought out during these periods.

The vast majority of the spring annuals, shrubs and trees are the same species found in coastal Santa Barbara and Ventura Counties, as would be expected. Just a few insular endemic plant species were noted. Of

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these, primarily three were examined extensively for Rhopalocera: Catalina Ironwood, *Lyonothamnus floribundus* (Rosaceae); Saint Catherine's Lace, *Eriogonum giganteum*; and Channel Buckwheat, *E. arborescens* (Polygonaceae). Although some butterflies visited these for nectar, none seemed to be associated with them as obligate larval hosts. In the 1978 survey, Nymphalidae ova and larvae were found on introduced *Lavatera assurgentiflora* (Malvaceae), endemic to other northern Channel Islands, and larvae on the more widespread *Baccharis plummerae* (Compositae).

In the following species treatment, the food-plants are only mentioned where considered significant. The hosts of the Rhopalocera (whether present or absent on S.C.I.) of southern California are recorded by Emmel & Emmel (1973).

Fifteen separate localities were surveyed on the island in 1966 — a few only once or twice and the more productive areas many times. Attempts were made to visit all accessible areas from the west end to the east, shorelines, canyons, streams, hillsides, ridges, disturbed fields and waste-weedy situations.

List of species

HESPERIIDAE: Hesperiinae

1. *Ochlodes s. sylvanoides* (Boisduval): A most unusual event was finding this skipper in spring flight. First taken on 30 April at Christi Beach, it was quite common throughout the island in early June 1966. In mainland California this species is generally a midsummer flyer, increasing in numbers by early autumn. Fresh specimens were also found at the more "usual" time of 1 Aug. 1969 (DW), but the flight had ceased by late Sept. 1978, a time of abundance on the mainland (JAP).

2. *Polites s. sabuleti* (Boisduval): Quite scarce on the island — one taken 2 mi. east of Christi Ranch and another at Christi Beach on 30 April 1966. The most characteristic habitats on the mainland are sandy areas near the coast, the flight period being April to September (Emmel & Emmel, 1973), and it can become common in urban and waste-weedy areas, with personal records from March to November.

HESPERIIDAE: Pyrginae

3. *Erynnis t. tristis* (Boisduval): Appeared to be generally scarce, but possibly an artifact of sampling. Ridges and higher points were not surveyed as frequently, and this species is often a hilltopper. It was taken sparingly in April, May and June 1966 at scattered locales. The species was quite common in late June 1978 (GG), and a single ♂ was taken late

as 1 Aug. 1969 (DW). The abundance of *E. tristis* on S.C.I. is similar to the Coast Ranges of California, and the dates are encompassed by the March to Sept. flight of this multivoltine species.

PAPILIONIDAE

4. *Papilio z. zelicaon* (Lucas): Rather scarce on S.C.I. in 1966 compared to lowland California. It was found along Albert's Ridge, 27 April, the ridge south of Chinese Harbor and along Prisoner's Harbor Creek, 9 June 1966. However, it was common by late June 1978 (GG), with larvae and pupae abundant on *Foeniculum vulgare* (Umbelliferae). Several adults on S.C.I., 1 Aug. 1969 (DW).

5. *Papilio eurymedon* (Lucas): Found throughout the island, April, May and June 1966 — on hilltops, ridges and along streams. It was very common and widespread in late June 1978 (GG), and still in flight by early Aug. 1969 (DW). It seems to occur in about the same numbers and habitats as on the mainland during the same time periods.

PIERIDAE

6. *Pieris p. protodice* Boisduval & Leconte: Only two males were taken — in a field of mustard, Upper Central Valley on 8 June 1966. This highly vagile species was expected in greater numbers. By late June 1978 it was more common, but not everywhere on the island (GG). In some seasons, *P. protodice* can become very common in most of California, and occurs in much of the continental United States.

7. *Pieris rapae* (Linnaeus): Although not found in the 1966 surveys, it was taken on 1 Aug. 1969 (DW), and in late June 1978 it was not scarce at all in the Central Valley (GG). *P. rapae* can be in adult flight every month of the year in southern California. It was introduced into Quebec, Canada from Europe in about 1860. It is now present in the Hawaiian Islands and many other islands of the Pacific (Howe, 1975). It was introduced accidently to New Zealand in 1930, and to Australia in 1939 (Common & Waterhouse, 1972).

8. *Colias e. eurytheme* Boisduval: Present in April, May and June 1966, but relatively scarce on the island. April examples included the early spring phenotype "ariadne" Edwards. Two males were taken on S.C.I. on 1 Aug. 1969 (DW). On the mainland, *C. eurytheme* can become extremely common, increasing from spring into autumn.

9. *Colias harfordii* Henry Edwards: Although not found in 1966, it was very common in parts of S.C.I., especially the Coches Prietos area, late June 1978 (GG). One mature larva was on *Lotus scoparius* (Leguminosae), Ridge Road near Upper Laguna Canyon (GG). This

species is found in cismontane southern California from San Diego to Kern Counties, but does not go much north of Santa Barbara County in the Coast Range (Emmel & Emmel, 1973).

10. *Anthocharis sara gunderi* Ingham: This was the only endemic found on Santa Cruz Island. It was extremely abundant in April and May 1966, mostly at Prisoner's Harbor, Prisoner's Harbor Creek and in the Central Valley. At times *gunderi* was much more common than one would find *A. sara* Lucas (or spring form "reakirtii" Edwards) at a single time or place on the mainland. Adults were again taken 14-16 March 1969 (O & P), generally along Prisoner's Harbor Creek.

LYCAENIDAE: Theclinae

11. *Satyrium s. saepium* (Boisduval): Earliest in the season on Albert's Ridge, 27 April 1966, and by June distributed both along ridges and the lowland areas. It was very common along Ridge Road, late June 1978 (GG). This species was in comparable numbers and habitats as in the chaparral areas of California.

12. *Callophrys d. dumetorum* (Boisduval): Near the end of its flight period, a few worn females were taken in April 1966 — Upper Central Valley, Canada Cervada and Prisoner's Harbor. Fresher examples were found along Prisoner's Harbor Creek, 14-16 March 1969 (O & P). This hair-streak is univoltine with a relatively short flight period. Throughout its extensive range in California, most records are in March and early April (Gorelick, 1971; Langston, 1975).

13. *Strymon melinus pudica* (Henry Edwards): Generally distributed on the island and more common in 1966 and 1978 than usually found in most parts of the western United States. Adults were in flight by mid-March 1969 (O & P), and still present by early Aug. 1969 (DW). *S. melinus pudica* was very common everywhere on S.C.I. in late June 1978 (GG), with numerous hosts noted. Perhaps its abundance on the northern Channel Islands may have prevented by competitive exclusion the establishment of *Strymon avalona* (Wright), known only from Santa Catalina Island (Emmel & Emmel, 1973).

LYCAENIDAE: Lycaeninae

14. *Lycaena helloides* (Boisduval): A single ♀ on deposit in the Natural History, 1 Aug. 1969 (DW) are the early examples from S.C.I. At Prisoner's Harbor, 7 ♂♂ & 5 ♀♀ were taken by Powell, 25, 29 Sept. 1978. This copper is widely distributed through much of the western U. S., including cismontane southern California. However, it has recently become scarce in much of southern California due to habitat destruction by urbanization (Emmel & Emmel, 1973).

LYCAENIDAE, Plebejinae

15. *Brephidium exilis* (Boisduval): Early specimens at Valley Anchorage on 27 April, and at Christi Beach, 30 April 1966. It was in greater numbers by 9 June in Eagle Canyon. It was found again in early Aug. 1969 (DW), and very common in late June 1978 at Coches Prietos Harbor (GG). *B. exilis* was in about the same habitats as in lowland California, its numbers increasing from spring into summer. First found on Oahu, Hawaii, in the summer of 1978 (Riotte & Uchida, 1979).

16. *Leptotes marina* (Reakirt): Two ♀♀ were taken at Prisoner's Harbor on 10 June 1966. This blue can be abundant in urban areas and lower canyons of southern California, especially in summer and fall. It could become more numerous on S.C.I. later in the season with numerous legumes as suitable hosts.

17. *Plebejus a. acmon* (Westwood & Hewitson): In April, May and June 1966 only eight specimens were taken at three separate locations on S.C.I. Some were nectaring on the endemics *Eriogonum giganteum* and *E. arborescens,* but not particularly attracted to these large buckwheats in relation to legumes and other plants in the areas. This multivoltine species was found from mid-March 1969 (O & P) to early Aug. 1969 (DW). It was very abundant in late June 1978 (GG), especially on the south side of S.C.I. near the coast. *P. acmon* can be very common in similar habitats throughout the western U.S.

18. *Everes amyntula* (Boisduval): Both sexes were very abundant at several places on the island, April, May and June 1966. It has been found in good numbers at other seasons (CR), but in some seasons (1969, 1978) none were observed. It is possible that wide fluctuations may occur in the island populations. Although distributed throughout the Pacific States (Downey *in* Howe, 1975), *E. amyntula* is seldom found in such vast numbers as on Santa Cruz Island in 1966.

19. *Glaucopsyche lygdamus australis* Grinnell: Near the end of its flight period, only four were taken on S.C.I. in April 1966 at Upper Central Valley, Cañada Cervada and Prisoner's Harbor. It was also found along Prisoner's Harbor Creek, mid-March 1969 (O & P). This univoltine spring-flier can become rather common in cismontane southern California and Baja California, Mexico (Langston, 1969).

20. *Celastrina argiolus echo* (Edwards): Generally distributed both along ridges and the lowland stream areas in 1966. A few adults were observed around Catalina Ironwood, but not significantly more than around other trees and shrubs. A single late-flying ♀ was taken 1 Aug.

1969 (DW). It was very common and widespread in late June 1978 (GG). This blue was in about the same numbers and situations as found in mainland California.

NYMPHALIDAE

21. *Adelpha bredowii californica* (Butler): Although the Coast Live Oak is abundant on the island, only three *Adelpha* were collected in 1966, with very few others observed — late April and early June at Prisoner's Harbor and the Central Valley. It was more common in late June 1978, Prisoner's Harbor Creek (GG), and worn by early Aug. 1969 (DW). Its scarcity in the spring is not considered significant as there are wide areas in California where it is uncommon at this time of year.

22. *Vanessa atalanta rubria* (Fruhstorfer): Noted in the Upper Central Valey and at Prisoner's Harbor in April, May and June 1966. Only a few around Prisoner's Harbor, late June 1978 (GG). It was not found in other parts of the island. Although scarce, its numbers were typical of many areas in the Northern Hemisphere. It has been introduced to the Hawaiian Islands, with the nominate *atalanta* established in New Zealand (Clench *in* Howe, 1975).

23. *Cynthia virginiensis* (Drury): Of all the VANESSINAE, this one was by far the most abundant. It was more common at Prisoner's Harbor and the Central Valley in April, May and June 1966 than usually found in most areas of California. Present in Aug. 1969 (DW), and extremely common everywhere on S.C.I., late June 1978 (GG), with larvae found on *Gnaphalium* (Compositae). Wide-ranging in the Americas, *C. virginiensis* has become naturalized on the Hawaiian Islands (Clench *in* Howe, 1975).

24. *Cynthia cardui* (Linnaeus): A very fresh ♀ (indicating a resident breeding population) was taken in the Upper Central Valley on 26 April. It was also found at Christi Beach on 30 April, and Prisoner's Harbor, 1 May 1966. This species was scarce in late June 1978 (GG), with just a few seen in the Central Valley. Its numbers were about the same as would be expected in California in non-migratory seasons. *C. cardui* is now known in Hawaii, Malaysia, Java, and Sumatra as part of its almost worldwide distribution (Clench *in* Howe, 1975).

25. *Cynthia annabella* Field: Taken in the Upper Central Valley in April 1966. Found in mid-March 1969, Prisoner's Harbor Creek (O & P), and early Aug. 1969 on S.C.I. (DW). It was fairly common between Prisoner's Harbor and the U.C. Field Station, late June 1978 (GG), with ova and larvae on cultivated *Lavatera assurgentiflora* (Malvaceae).

C. annabella is common in much of California, with adult records all months of the year.

26. *Junonia coenia* (Hubner): A single ♀ was collected in a waste-weedy area near Prisoner's Harbor on 1 May 1966. However, very common all over the island, late June 1978 (GG). *J. coenia* is often common in lowland southern to northern California, with adult records every month of the year.

27. *Nymphalis antiopa* (Linnaeus): A single ♀ in the Santa Barbara Museum of Natural History was taken at the mouth of Cañada Islay, 11 May 1970 (DW). *N. antiopa* occurs throughout the Holarctic Region. In the Western Hemisphere it ranges from Alaska to Venezuela (Gorelick *in* Howe, 1975).

28. *Chlosyne gabbii* (Behr): Common at several localities in the central and eastern parts of the island — April, May and June 1966. On some days along Prisoner's Harbor Creek and the Central Valley it was extremely abundant, patrolling along streams and washes, and nectaring on many types of flowers, especially *Baccharis plummerae* (Compositae). Adults were in flight as early as 14-16 March 1969 (O&P), along Prisoner's Habor Creek; very common as late as 23-30 June 1978 (GG) in the Central Valley. Gorelick also took a few larvae near Prisoner's Harbor on *B. plummerae* — a new host since Emmel & Emmel (1973). *C. gabbii* was much more numerous than ever observed by me in southern or central California.

29. *Euphydryas c. chalcedona* (Doubleday): One of its preferred foodplants, *Diplacus* (Scrophulariaceae), was growing throughout much of the island. However, only five *E. chalcedona* were taken — as singletons at five separate localities, late April and early May 1966. In other seasons it has been found found abundantly on S.C.I., as it occurs in much of California where it is found in very large numbers and easily netted.

30. *Speyeria callippe comstocki* (Gunder): On a knoll south of Chinese Harbor two fresh ♂♂ were taken and two more observed on 9 June 1966. Two ♂♂ and 2 ♀♀ were found again on the same hilltop, 28 June 1978 (GG). Possibly this species is scarce or restricted to just one or a few colonies on S.C.I. In comparison to mainland southern California, this correlates as there are many areas where it is not found, and others where it can be rather common.

DANAIDAE

31. *Danaus p. plexippus* (Linnaeus): Worn hibernants were in the Prisoner's Harbor area on 1 May and 9 June 1966. Fresh adults, both

sexes in late June 1978 (GG), mostly in the Central Valley, with larvae on *Asclepias fascicularis* near Prisoner's Harbor. The breeding populations on S.C.I. were probably initiated from "fly-overs." *D. plexippus* has gradually extended its range across the Pacific Ocean from North America. In the Hawaiian Islands it can be very abundant (Langston, 1979), and it is said to have reached Australia first about 1870 (Common & Waterhouse, 1972).

SATYRIDAE

32. *Cercyonis sthenele silvestris* (Edwards): The populations on S.C.I. differ from the *silvestris* of cismontane southern California sufficiently that they probably warrant a name (Remington, 1978). These more whitish "*sthenele*-type" were initially found near the west end of S.C.I. (CR). Taken 1 Aug. 1969 (DW), and on 27, 29 June 1978 it was found further east on the island (GG). Common: 1) on trail from U.C. Field Station to Ridge Rd.; 2) along Ridge Rd. on south side of island; 3) above Coches Prietos Harbor on the south side; and 4) occasional 1-2 mi. east of the Field Station in the Central Valley (GG). Although phenotypically different, its numbers and flight period compares to *silvestris* in much of coastal southern to northern California.

Additional species in California

Several species of Rhopalocera known commonly in Los Angeles, Ventura and Santa Barbara Counties, California were not found on Santa Cruz Island in the 1966, 1969 and 1978 surveys. Their absence was notable as some can be very much in evidence not only in California, but the entire western United States and/or the North Temperate Zone in general.

HESPERIIDAE

Ochlodes a. agricola (Boisduval) was taken in Santa Barbara County two days before the April 1966 trip to S.C.I. This species was expected in the spring on the island rather than *O. sylvanoides* which normally flies on the mainland in summer and fall. [2]Several specimens were taken 26-29 Sept. 1978 at four separate localities by J. A. Powell & Marion E. Buegler. With the addition of *albescens*, 33 species are known from S.C.I. at latest count. *Pyrgus communis albescens* (Plotz) is especially common in the lowlands of California, particularly in disturbed areas, with captures recorded every month of the year. A black-fringed dusky-wing, such as *Erynnis propertius* (Scudder & Burgess) was not observed. Live Oak trees were plentiful, and the single brood adults of *propertius* are in flight from March to June.

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[2] Several specimens were taken 26-29 Sept. 1978 at four separate localities by J. A. Powell & Marion E. Buegler. With the addition of *albescens*, 33 species are known from S.C.I. at latest count.

PAPILIONIDAE

Papilio r. rutulus Lucas is large and conspicuous, and would certainly be noticed on S.C.I. if present. It is common along streams, city parks and urban areas in California and much of the western United States. March to September is the usual flight period in coastal lowland California.

PIERIDAE

Colias eurydice Boisduval has not been found on S.C.I., although this fast-flier is found in the foothills and canyons from northern to southern California. A subspecies of *Anthocaris cethura* could be expected on the northern Channel Islands, as a correlation with the endemic *A. cethura catalina* Meadows known only from Santa Catalina Island, Los Angeles County.

RIODINIDAE

No examples of Riodinidae were found on S.C.I. The most logical candidate would be *Apodemia mormo virgulti* (Behr), which is found throughout the chaparral zones of cismontane southern California both in the spring and late summer to fall. Although several species of *Eriogonum* were present, its preferred host, *E. fasciculatum* was not observed on the island.

LYCAENIDAE

Within the Subfamily THECLINAE, several species of hair-streaks would be possible. Three species of theclines (one in great abundance) were actually present. *Incisalia augustinus iroides* (Boisduval) could be expected in the early spring, and *Satyrium s. sylvinus* (Boisduval) in late spring and summer.

Only one species of the Subfamily LYCAENINAE was present. Judging by presence of hosts and times of year, at least two more were expected: *Lycaena gorgon* (Boisduval) and *L. x. xanthoides* (Boisduval).

The Subfamily PLEBEJINAE was well represented on S.C.I. — six species in six separate genera. Searches were made for one in a seventh genus. *Euphilotes battoides bernardino* (Barnes & McDunnough) was collected in Ventura County the day before the April 1966 trip to S.C.I., and in Santa Barbara County the day before the June 1966 trip. Two species of large shrub-type *Eriogonum* were growing on the island, but its preferred host, *E. fasciculatum*, was not observed. This blue is common and well distributed in cismontane southern California (Shields, 1977; Langston, 1965, map 1). *Plebejus icarioides evius*

(Boisduval) can be common in mainland Santa Barbara County and generally in the mountains of southern California, with adults from May to July.

NYMPHALIDAE

Limenitis l. lorquini (Boisduval) and *Polygonia s. satyrus* (Edwards) were not found in the canyons or stream areas, even though willows and nettles were present in several parts of S.C.I. *Phyciodes m. mylitta* (Edwards) is found from British Columbia to Baja California. It is multivoltine at the lower elevations. In coastal lowland California *P. mylitta* is found in many habitats from early spring into late autumn. A subspecies of *Euphydryas editha* (Boisduval) occurs on Santa Rosa Island in the absence of *E. chalcedona* (Emmel & Emmel, 1975; S. Miller, per. com.). The nominate *editha* and at least three subspecies are known from central and southern California (Emmel & Emmel, 1973), but nothing in this complex recorded from S.C.I.

SATYRIDAE

Coenonympha c. california Westwood was surprisingly absent from Santa Cruz Island. This ubiquitous species is often abundant on grassy hillsides of coastal California from February to October.

Discussion and Summary

Based upon surveys of Santa Cruz island, Santa Barbara County, California [1939, 1966, 1967, 1970 & 1978], fewer species of Rhopalocera were found than would be expected. With at least token surveys from essentially mid-March to late Sept. (although in different years), it appears the maximum number of possible species have been recorded. In comparison to mainland California (with emphasis on Los Angeles, Ventura and Santa Barbara Counties) this includes the adult flight periods of almost all of the univoltine species. Surveying earlier in the spring would possibly be hampered by inclement weather, and it would be too early for many of the species to emerge as adults. Conditions became quite dry by August, at which time the adult flight of most of the univoltine species has already ceased.

A total of 33 species were collected and observed in six different years, including the extremes of 14 March and 1 Aug. in a single season (1969). At least five species were found in greater numbers on Santa Cruz Island than on the mainland under comparable habitats during the same time periods. These were: *Anthocaris sara gunderi, Strymon melinus pudica, Everes amyntula, Cynthia virginiensis* and the very numerous *Chlosyne gabbii.*

The only endemic, *A. sara gunderi,* was extremely abundant in April and May 1966. The remaining 32 taxa are all well documented in Santa Barbara and Ventura Counties. Most are widespread throughout California, with many ranging in the western United States, and a few being Nearctic or even Holarctic.

A surprising occurrence was the spring flight of *Ochlodes sylvanoides.* First taken on 30 April 1966, it was quite common throughout the island by early June. In a different season, 1969, fresh examples were found in early August, whereas not flying in late Sept. 1978 when common on the mainland.

The most notable species that are apparently absent from Santa Cruz Island are *Papilio rutulus, Incisalia augustinus iroides, Limenitis lorquini, Phyciodes mylitta* and *Coenonympha california.*

The lack of certain species appears to be due to its being an island *per se,* combined with overgrazing by both cattle and feral goats. Wide areas of the island are somewhat barren of native vegetation. Other parts have been fenced off and the flora seems to be recovering. Weedy annual and perennial plants have invaded some locales, especially the grazed areas. In instances where they outcompete the native plants, this would tend to eliminate or reduce any endemic Lepidoptera that may have been present in the past. On the other hand, this phenomenon would favor such butterflies as *Papilio zelicaon, Pieris rapae, Cynthia annabella* and *Junoria coenia.*

Several species on Santa Cruz Island also occur in the Hawaiian Islands, with some ranging across the Pacific Ocean as far as Australia, New Zealand and the Orient. These comparisons were made as the more isolated islands have fewer species, as would be expected. For example, the entire Hawaiian chain has only 15 species of Rhopalocera — 2 endemics, 13 imports (Langston, 1979; Riotte & Uchida, 1979). Santa Cruz Island (with 33 species) and the Channel Islands in general, being just offshore from a continental land mass have a much richer fauna than these isolated islands — but still less than half the number on the relatively close mainland.

Editors Note:

Reference to *A. sara gunderi* is open to interpretation. Langston (*in litt.*) recognizes the applicability of *gunderi* based upon Emmel and Emmel (1973 *op. cit.*). Use of *gunderi* in the paper is solely dependent on the Emmel and Emmel reference. In the meantime John Emmel examined SCI specimens and agreed they were best referred to ssp. *reakirtii.* Langston (*in litt.*) concurs with the concept, in addition to a reviewer and the editor. The S.C.I. specimens can not be easily confused with *gunderi* and appear superficially identical with *reakirtii.* The statements about "endemism" of "*A. sara gunderi*" are therefore open to question on the opinion of all concerned.

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Territorial Behavior of the Red Admiral, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae)

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Although butterflies are not equipped with means to inflict injury, the intensity with which males of many species pursue conspecifics, butterflies of other species, birds and even lepidopterists suggests that some butterflies are highly aggressive (Silberglied, 1977). Recently there has been an increasing number of reports that the apparently aggressive behavior of some species is part of territorial behavior (Baker, 1972; Douwes, 1975; Silberglied, 1977; Davies, 1978).

Scott (1974) suggests that butterflies are not aggressive and not territorial. He believes that what appear to be aggressive attacks are simply males' attempts to determine the species and sex of flying objects perceived from a perch. Because male butterflies do not always return to the same perch and usually do not occupy the same perch on successive days, Scott questions whether male butterflies of any species occupy fixed areas.

In this study, we described behavior of *V. atalanta* males which we believe represents true territorial behavior, namely defense of a fixed site.

Materials and Methods

Observations were carried out at various locations on the Iowa State University campus. Butterflies of the spring brood[1] were observed on 8 days between May 4 and 17, 1977, 8 days between May 18 and 26, 1978, and 8 days between June 9 and 21, 1978. Butterflies were identified by unique characters (raggedness of wings, size, color) and by marking descaled areas of one wing's ventral side with spots of non-toxic acrylic paint. Thirty-six territorial butterflies were captured and sexed by gently squeezing the tip of the abdomen to extrude the genitalia. After sexing and/or marking, captured butterflies were released under the net and gently directed to the ground or sidewalk near the resting spot of capture. However, 41 of 43 males flew away immedately after release.

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[1] In 1978, the first adult butterfly was spotted on May 18 and the last territorial male was seen on June 26. Within 2 weeks, we again saw adults, apparently members of a summer brood.

Results

Although individual *V. atalanta* were observed flying through territorial sites as early as 0900 hr, territorial behavior was never observed earlier than 1700 hr (CST). Within 30 min after the first territory was established, the number of territories increased and their boundaries became sharply defined. Intermittent flights (patrols) by territory occupants traced territorial boundaries (Fig. 1). Boundary lines were confirmed by points at which butterflies stopped pursuing floating objects, birds and other species of butterflies. Males usually occupied territories until 1830-1930 hr but left earlier on cool or overcast days.

Usually one male occupied and successfully defended his territory for a 2-2½ hr period. Since marked males almost always flew away immediately after release, discrimination between occupant and intruders depended on our ability to identify unmarked butterflies. In eight cases (which included two previously marked butterflies), we could easily identify the original resident of a territory and determine whether these butterflies successfully defended their territories for the total daily territorial period, or were displaced. In six cases, the initial occupants were not displaced; each occupant drove off one to 13 intruders. The other two males eventually lost their territories to intruders. One male was displaced after his third flight interaction with an intruder. The other male defended his territory successfully eight times before being driven off during his ninth flight interaction.

Different males tended to occupy the same territories on different evenings and even during different years. Butterflies occupying a territory on a particular day rarely returned at a later date. Of 39 individually identified males (35 marked, four identified by unique morphological characteristics) in 1977 (nine males) and 1978 (30 males), only two males returned to the same or adjacent territories on subsequent evenings.[2]

Territories were roughly elliptical in shape, varying from 12-24 m in length and 4-13 m in width (Fig. 1). Each territory had a core area, an area common to a territory mapped on successive days (Fig. 2). The area peripheral to the core area varied with different territorial

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[2] Both males returned under unusual conditions. One male, marked on May 23, 1978, roosted in a tree within his territory. This was the only male ever seen to roost in a territory. He was observed the next morning at 0900 hr, had departed by 1000, and returned to the territory by 1730.

The other male was marked in territory #1 on June 9, 1978. He was seen in territory #1 on two different occasions on June 19, 1978 for periods of 2 and 10 min before being displaced. This male reappeared in territory #1 only after at least eight former territorial owners had been marked and fled the territory.

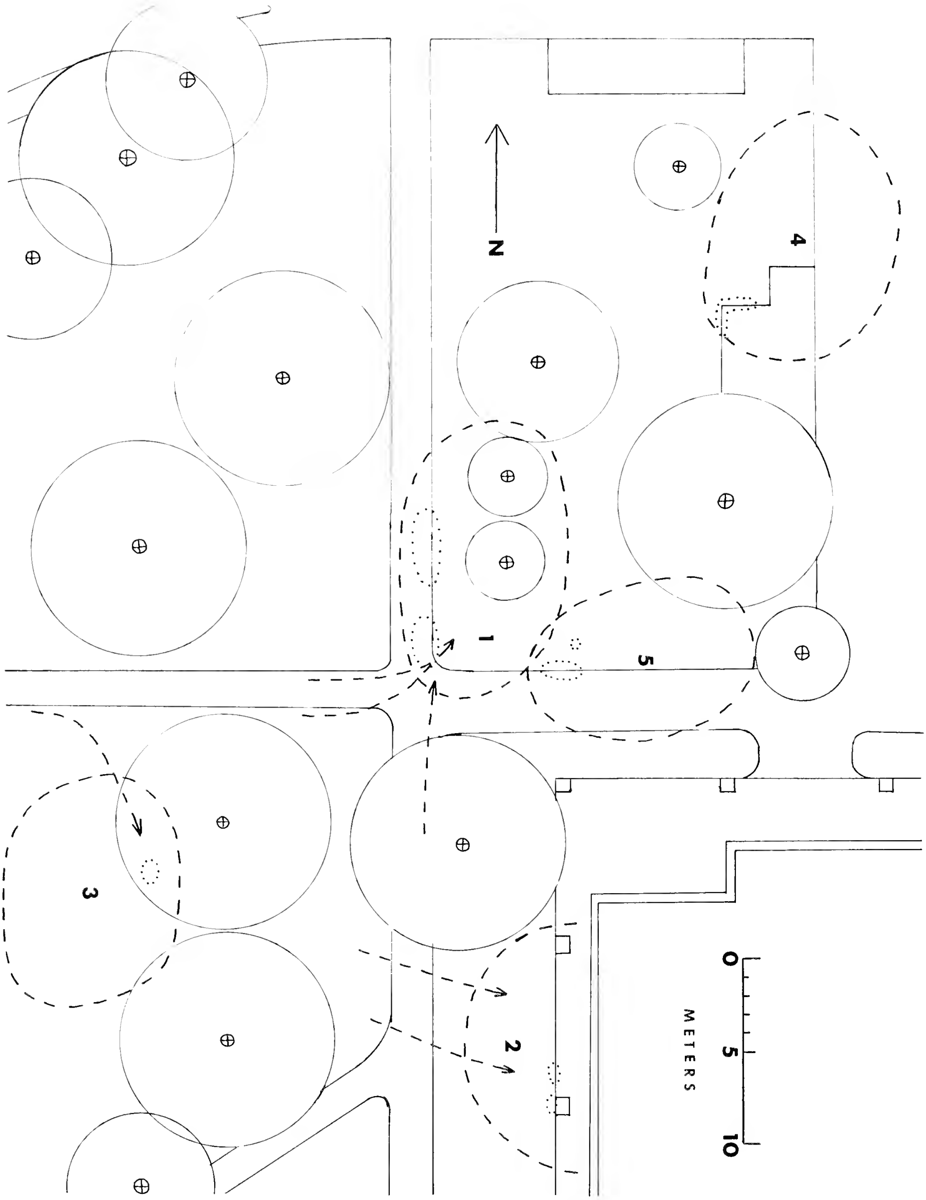


Fig. 1 Territories in courtyard on ISU campus, May 1977. Dashed lines - typical, territory boundaries. Dotted lines - shape, size and location of resting spots within territories. Arrows — routes along which intruders frequently entered territories. Solid lines — trees, sidewalks, buildings.

owners. In some cases, even the peripheral areas were similar for two or more different territorial owners.

Each territory contained one or two fixed resting spots which lay within core areas and were similar for all territorial holders of a given territory (Figs. 1, 2). Not only did each territorial owner consistently return to the same spot, but intruders capturing that territory on the same night, and occupants on successive nights (even successive years) rested on approximately the same spot. Resting spots were usually on the ground (sidewalk, rocks, or patches of bare ground), occasionally on the walls of buildings, or, less often, on a bush or low branch of a tree. Resting spots on sidewalks were ellipses 1-2½ m long, 30-60 cm wide with major axes parallel to the long axis of the sidewalk butterflies spent 70-90% of their time resting within their territories. Resting spots on walls were 30 cm to 2 m in diameter, located 30 cm to 3.7 m up the wall. Except when interactions were unusually frequent, butterflies spent 70-90% of their time resting within their territories.

Territories were found along sidewalk edges, along sunlit, western-facing walls and on open sunlit lawns (Fig. 1). The major axes of some territories pointed toward trees or corners of buildings lying some distance from the territories.

Normally *V. atalanta* males spent 4-12% of their time patrolling their territories, flying 7-30 patrols/hr. However, one male occupying a territory on an open sunlit lawn patrolled continuously for the last 1¼ hr of his territorial period. During a single patrol, a male traced a flight path two to six times in a period of 5-60 sec before returning to his resting spot. Butterflies usually patrolled along the edge of a territory about 1½ m above the ground. One butterfly occupying territory #2 (Fig. 1), repeatedly climbed approximately 9 m up the wall in a winding fashion.

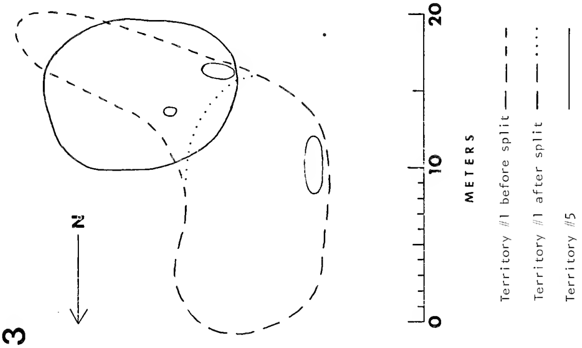
When large objects (white cloth bag, spiral notebook) were placed within territories, patrolling butterflies changed course and repeatedly flew around these objects. Sometimes butterflies hovered above objects or perched on them briefly before resuming patrolling or returning to their resting spots. During June 1978, workers dug a hole within the core area of territory #1 (Fig. 1) and placed a fence around it. Butterflies avoided the fence and territorial boundaries were restricted to within a meter of the edge of the sidwalk.

Some territories may be considered optimal because of considerably greater frequency of occupancy. Frequency of occupation of each territory was similar during 1977 and 1978. During a total observation period of 20 days in May 1977 and May and June 1978, percentage of occupancy was 85% for territory #1, 60% for territory #2, 25% for territory #3, 20% for territory #4 and 15% for territory #5. Territory #8, observed for 12 days during May and June 1978, was occupied 83.3% of the time. Territories #1, 2 and 8 were preferred areas and therefore optimal.

The highest rates of resident-intruder interactions (up to 21/hr) occurred in optimal territories. Such competition occasionally resulted in two or more males claiming the same territory. A butterfly claimed a territory if he rested within that territory and flew or attempted to fly a pattern which defined territorial boundaries. When more than one butterfly rested in a territory, an occupant who flew up, presumably in an attempt to patrol his territory, was immediately chased by another occupant. The results of such competition were 1) establishment of an adjacent territory (two cases, Fig. 2), 2)splitting of a territory into two smaller territories (three cases, Fig.3), 3) one butterfly was driven off (occurred only once), and 4) intermittent chases occurred until all butterflies flew away at the end of the daily territorial period (two cases). It is likely that occupation of any suboptimal territory (e.g., territories #4 and #5, Fig. 1) was a result of competition for a nearby optimal territory (e.g., territory #1, Fig. 1).

Territorial butterflies spent 5-15% of their time interacting with other individuals entering their territories. The rate of interaction ranged from 1.62-21/hr, but was commonly between 10-15/hr. Intruders typically entered a territory along specific routes, usually from the west (Fig. 1), flying from 30-130 cm above the ground (Fig. 4). The resting or patrolling butterfly then flew up or changed course, rushed at the intruder from underneath, and sometimes hovered above the intruder for 1-2 sec before chasing it along an erratic path 1-2 m above the ground for 5-20 sec. Sometimes the butterflies flew through the dense foliage of low branches. Then the territorial butterfly closed to within 30 cm of the other and began chasing it along one to seven turns of an ascending helical path, 4-9 m in diameter, most often in a counterclockwise direction as seen from below. When they had climbed to treetop level, some 10-18 m above the ground, the territory holder broke off the chase and dropped into its territory (Fig. 4). With close observation of chaser, we were able to distinguish territory owner from intruder an estimated 95% of the time. These interactions usually lasted 10-30 sec but some were as long as 60 sec.

After a chase, the intruder usually was lost from sight. When observed, the intruder usually flew a short distance from the top of the helix before descending toward the ground and flying away. During frequent male-male interactions (10-21/hr), 5-8% of the intruders descended within a few meters of the territory and re-entered it immediately. During periods of high interaction frequency, an intruder may enter a territory while the owner is chasing another butterfly. We saw this three times in territory #2 (Fig. 1) on May 5, 1977.



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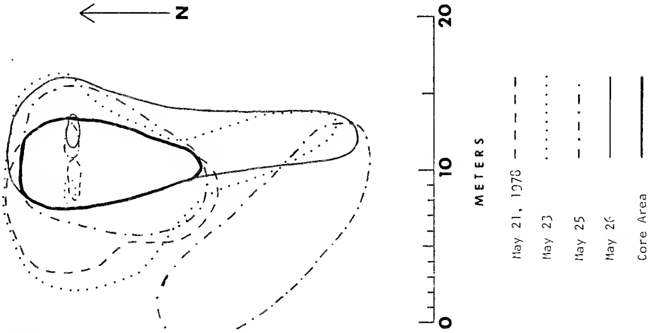

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Fig. 2. Core and peripheral areas of a territory (#8). Adjacent territory occupied by second butterfly on May 25, 1978.

Fig. 3. Splitting of a territory as a result of competitive interactions of two males. Small ovals within territories are resting spots.

The frequency and lag time of reoccupation of a territory after release and departure of marked males is a measure of the availability of males without territories and possibly the intensity of competition for optimal territories. On June 19, 1978, we captured and marked, or chased away, 18 males in territory #1 (Fig. 1) between 1305 and 1910 hr. All males were replaced within a few sec. to 5 min. and only one replacee was a returnee marked 13 min. earlier in the same territory.

No *V. atalanta* were seen to feed, roost (one exception under unusual circumstances), oviposit or mate in defended territories. *V. atalanta* is not sexually dimorphic and all individuals that we sexed were males. We observed few behaviors, other than resting, chasing intruders and patrolling, which could be used to speculate about the function of *V. atalanta* territories.

Intermittently males opened their wings holding them in a horizontal position revealing the brightly colored dorsal side. This could be an aggressive or courtship display. Although no data were recorded, it appeared that males in sunspots held their wings horizontally more frequently than males not on sunny resting spots. This suggests that *V. atalanta* males may open their wings to help maintain or raise body temperature.

Discussion

According to Baker (1972), the nymphalid butterflies *Inachis io* and *Aglais urticae* establish breeding territories along visual lines of demarcation (i.e., hedges, walls or rows or trees) along which females are likely to fly. The most active (optimal) territories of *V. atalanta* were along sidewalks and sides of buildings which probably form strong linear visual patterns to flying butterflies. A line of two or more trees may have been necessary visual input for butterflies forming territories in open areas of the university lawn. Flight paths of intruders were similar for a given territory, suggesting that intruders were using the same visual orientation cues and probably the same used by the territory owner.

The locations of territorial resting spots and flight paths demarcating territorial boundaries probably also depend upon visual cues. Occupation of the same territories, same resting spots and, in some cases, similar territorial boundaries by different butterflies on different days (even different years) is strong circumstantial evidence for a species response to visual cues. *V. atalanta's* responses to foreign objects (hovering above, perching upon or flying around them) suggests they became familiar with visual features of their territories.

Visual cues also appear to be important in the territorial behavior of dragonlies. As with resting spots of *V. atalanta,* perch sites of males of the dragonfly, *Hetaerina americana,* tend to be permanent. Territory owners and intruders that succeed in displacing owners generally rest on the same perch (Johnson, 1962).

Resting spots (sidewalk, rocks, bare spots of ground) of *V. atalanta* are invariably lighter than the immediate surroundings. This also may be true for *Vanessa annabella* Field (Dimock, 1978). The choice, by *V. atalanta* males, of such specific areas for resting spots suggests use of visual signals other than lightness of background. A light background probably camouflages resting males with wings held vertically. The same background would contrast with and enhance the possible display of the colorful, horizontally-held wings.

Fixity of resting spots may be related to intruders entering territories from specific directions. If intruder's flight paths are determined by certain visual features of territories, those territory holders which establish resting spots near these entry points would force intruders to pass through the most heavily defended parts of the territory thereby reducing the intruders' chances of occupying it.

Although most resting spots of *V. atalanta* remained fixed during the entire daily territorial period, a few butterflies changed their resting spots in order to occupy a spot of sunshine. The butterfly *Parage aegeria* also remains in moving sunlit spots on the forest floor (Davies, 1978). For *P. aegeria,* however, the sunspot is the territory. *V. atalanta* males only occupied sunspots within their territorial boundaries and only when the temperature was below 20° C. Changing resting spots in order to remain in sunlight at relatively low temperatures may be a mechanism to prevent heat loss.

V. atalanta's attacks on a variety of animate (including other species of butterflies) and inanimate objects (e.g., floating leaves) suggest that their chase response is not very specific. Although *V. atalanta* males do not chase birds or other species of butterflies in a vertical helix, they do pursue them to the territory's edge with obvious intensity darting around them and moving toward them repeatedly as if attacking. This apparently contrasts with territorial *P. aegeria* males (and males of many perching species; Scott, 1974), whose approaches to other species of butterflies are described by Davies (1978) as inspections.

Although such intense chasing of other species of butterflies seems a waste of energy, selective factors other than energy savings from chasing only conspecifics may be operating. The persistence with which a territorial *V. atalanta* chases a wide range of flying insects and birds could serve to 1) identify conspecifics and possibly sex of conspecifics, and/or 2) increase the rate at which birds and other insects leave the territory. If resting *V. atalanta* males cannot identify conspecifics, chasing off flying animals which they cannot differentiate from conspecifics should reduce their chances of chasing the same animal again. It is also possible that there have been, and may be in other areas, interspecific competitors for similar territorial sites. For example, Dimock (1978) reports that three species of *Vanessa* "congregate" on hilltops and other open sunny places where they chase one another along with unrelated butterflies, birds and other large insects.

The frequent interaction of two to five butterflies in optimal territories on sunny days, splitting of optimal territories or formation of adjacent suboptimal territories, and the rapid replacement of displaced territorial males, suggest that, at least on certain days, there is a low density of optimal territories. We have located only 10 territories on the ISU campus and no more than five are optimal. When optimal territories are limited, a non-territorial owner may occupy a suboptimal territory or contest for an optimal territory. Either strategy may result in approximately equivalent chances of obtaining a female (Parker, 1970).

Baker (1972) observed that, unlike *V. atalanta,* territorial *I. io* and *A. urticae* do not drop back into their territories after chasing intruders in a rapidly ascending spiral, but go into a series of dives and climbs along a path that carries them as far as 200 m away from the territory. In one respect, the long flight away from the territory is more advantageous than the helical interactions of *V. atalanta,* in that intruders would be less likely to find the territory again after chasing intruders in a rapidly ascending spiral, but go into a series of dives and climb along a path that carries them as far as 200 m away from the territory. In one respect, the long flight away from the territory is more advantageous than the helical interactions of *V. atalanta,* in that intruders would be less likely to find the territory again after having been chased off. However, such chases require the butterfly to spend time far from its territory, increasing the chances of a third butterfly occupying it.

The 10-18 m high helix of *V. atalanta* allows the territory holder to chase the intruder a relatively great distance upward without moving a large horizontal distance from its territory. If a third butterfly attempts to occupy the territory, the owner can (and did) break out of the chase, drop downward, and rush at the new intruder. At the same time, the first intruder may become disoriented in overhead branches. Perhaps interaction type is related to the habitat the butterfly occupies. In open areas, such as the fields where *I. io* and *A. urticae* set up territories (Baker, 1972), the long flight away from the territory might be more advantageous, while in areas with tree canopy, the helix may be preferable.

Baker (1972) reports that *I. io* and *A. urticae* males feed in the morning, set up territories in the afternoon (1130-1630 hr), leave territories to follow females, and mate at an evening roosting site. This behavioral time table very likely applies to *V. atalanta.* We have observed lone and aggregated *V. atalanta* feeding at various locations around Ames, Iowa between 0900 and 1700 hrs. Although we have observed no activity other than resting, patrolling and chasing, some chased intruders may have been females and males chasing them may not have returned to their territories. When helical chases were carefully observed, one male, probably the territorial owner, was seen to drop back into the territory in 95% of the chases. In the remaining 5% of the observations, males could have followed females rather than returning to their territories.

In the few reports of nymphalid males chasing females (Temple, 1953, Stride, 1956), the butterflies hover or quiver together before the male chases the females in a rapidly ascending spiral. Stride (1956) describes quivering of male and female *Hypolimnas missippus* (L.) before and throughout an ascending flight. We observed hovering on only two occasions, repeatedly during flight interactions within territory #9 on May 26, 1978 and within territory #2 on June 13, 1978. According to Temple (1953) *A. urticae* males chase females in ascending spirals and the flight paths of each sex are different. In *V. atalanta*, the flight patterns of the two or three butterflies ascending in a spiral or helix are always the same. It is possible that all helical chases we observed involved only males.

Like *V. atalanta,* most males of *I. io* (Baker, 1972) and two species of *Hamadryas* (Nymphalidae) (Ross, 1963) probably occupy territories or perches for one day or less. According to Baker (1972), *I. io* males move across the countryside, in a more or less straight line, from one feeding site to another until about midday when they select a suitable teritory. *V. atalanta* males also seem to move a great deal while feeding. Such movement would result in males occupying territories in new locations each day, which is consistent with our observations.

Scott (1974) suggests that before a butterfly species can be considered territorial "1) many males must remain at the same spot for a period of several days (also implied by Ross, 1963), 2) males must be able to quickly distinguish males from females, and 3) males must by intent drive other males from the area."

Noble's (1939) definition of a territory as a "defended area" has been restated by Brown (1975) as "... a fixed area from which intruders are excluded by some combination of advertisement ..., threat, and attack." This definition does not include Scott's (1974) requirement of territory occupation for "several days." *V. atalanta* males occupy and repeatedly defend (up to 21 times/hr) specific areas for periods up to 2 ½ hr.

Scott (1974) is critical of previous studies because they do not convince him that males consistently return to the same perch. *V. atalanta* territorial owners do consistently return to the same perch (resting spot). In addition *V. atalanta* males identify territories larger than resting spots by 1) outlining territory boundaries during numerous patrols, and 2) stopping at these boundaries when chasing birds or other butterfly species.

Scott's other two criteria deal with territorial defense. He believes that perched males pursue conspecifics and other flying animals, not to drive them from the territory, but to identify species and sex. However, Temple's (1952) description of courtship interaction of *A. urticae* is very different from Baker's (1972) description of territorial chases in the same species. This suggests that *A. urticae* males are able to distinguish an intruder's sex early in an interaction. Initially *V. atalanta* males sometimes hover and then chase an intruder along an erratic path. We suggest that sex and species recognition take place at this time after which the territorial male may 1) repeatedly dart at birds or other species of butterflies until they leave his territory, 2) chase inspecific males, and possible inspecific females, in a helical path, or 3) perform a yet undetermined flight path with a receptive female.

The evolution of territorial behavior in butterflies or any other animal is the result of increasing competition for access to one or more resources. In the case of butterflies, increasing competition for perching sites favorable to interception of females could lead to an increasing tendency to occupy specific areas and reduced time for species and sex recognition. Earlier sex and species identification would enable the territorial occupant to perform the behaviors appropriate to the type of intruder (e.g., driving conspecific males away in a vertical path) and return as quickly as possible to reoccupy his territory. Scott's (1974) unwillingness to accept territorial behavior in butterflies probably results from his experience with perching species whose behavior lies along the continuum between species that occupy many poorly defended perches in poorly defined areas and species whose behavior approaches but is not truly territorial. We believe that *V. atalanta* male exhibit territorial behavior because they occupy and defend fixed sites.

Summary

Vanessa atalanta (L.) males maintain territories during a 2-2½ hr period before dusk. A single male usually holds a territory during the territorial period but may be displaced by an intruder, especially after successive interactions. Territory owners seldom return on successive evenings. *V. atalanta* males probably move varying distances while feeding during the day and set up territories in different areas each afternoon.

The location, shape and components of territories are probably established with respect to visual features of the environment. Territories are established along strongly linear features (sidewalks, sides of buildings, possibly a line of two or more trees). Territorial boundaries, roughly elliptical in shape, are defined by intermittent flights or patrols. Territory owners occupy resting spots, within the territories, which are always lighter (bare ground, sidewalk, sunspot) than the surrounding area.

Each territory has a core area, an area common to a territory mapped on successive days. For each territory, the area peripheral to the core area may vary among territorial owners, but even the peripheral area may be similar for two or more territorial occupants. Within each territory core area, there are one or two resting spots or perches. The same spot(s) were used by all territorial owners observed during spring 1977 and 1978.

Territory owners leave their resting spots and intercept other butterflies when the intruders cross the territorial boundary. Territorial butterflies chase intruders along an ascending helical path above the territory. Birds and butterflies of other species are chased horizontally and only to the territorial boundary.

Some territories are occupied much more frequently than others. Such optimal territories are intruded upon frequently and intruders, after being chased away two or more times, may return and rest in the territory. Such competiton for an optimal territory may result in 1)

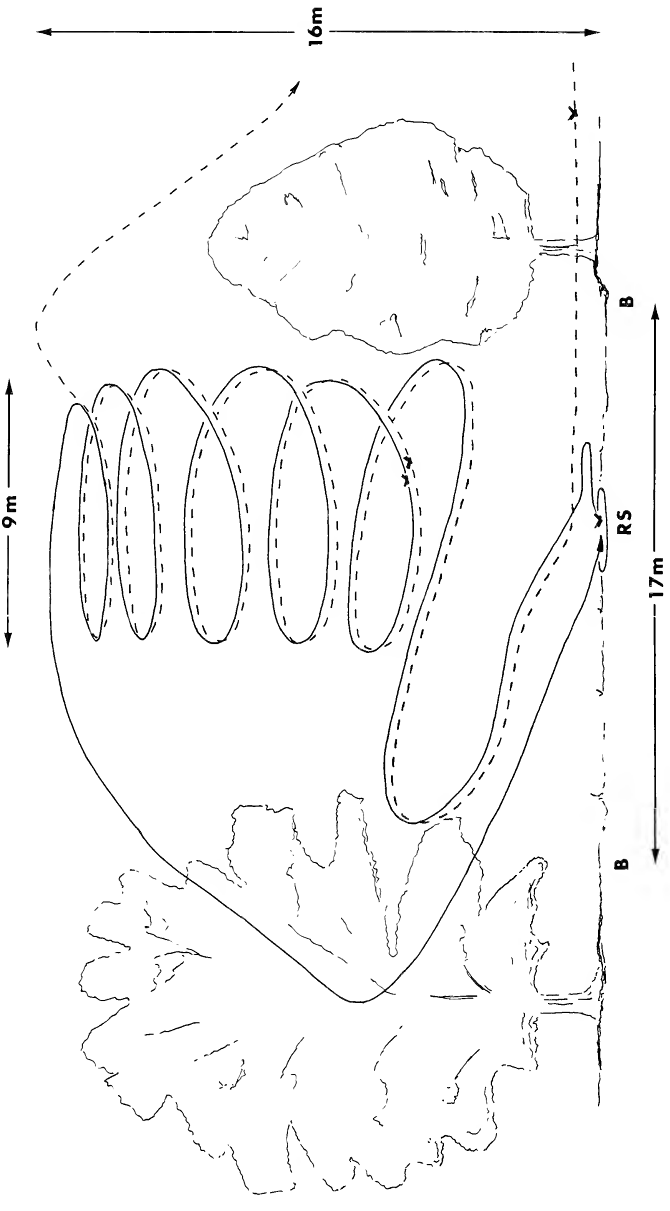

Fig. 4 Flight patterns during a typical interaction between two *V. atalanta* males. B — territory boundary; RS — resting spot; solid line — flight of territory occupant; dashed line — flight of intruder.

splitting of the territory into two smaller territories, 2) establishment of an adjacent territory, or 3) continued interaction until all butterflies leave at dusk.

The intensity of competition for optimal territories as well as rapid replacement of territorial owners driven from their territories suggests a low density of optimal territories. Territorial splitting, development of territories adjacent to optimal territories, and joint occupation of an opimal territory probably represent successful strategies of males who are not initial territory owners and who have failed to displace a male from an optimal territory.

Acknowledgments: We would like to thank Ken Johnson for the diagram of a territorial interaction between two *V. atalanta* males.

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Geographic variation in *Lycaena xanthoides*

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Abstract.—Fifteen wing characters analyzed from seven populations, and larval foodplant information, are used to correct an error in the systematics of the *Lycaena xanthoides* group. *L. x. xanthoides* and *L. x. editha*, formerly considered separate species, are closely related and connected by intermediate populations. *L. x. dione,* previously considered conspecific with *L. xanthoides*, is the most distinct entity. These allopatric subspecies form a cline from *L. x. dione* to *L. x. xanthoides* to several populations in California intermediate between *L. x. xanthoides* and *x. editha* to *x. editha* from California-Oregon to *x. editha* from the Rocky Mountains. The major gap in the cline is between *x. dione* and *x. xanthoides.* The cline is horseshoe-shaped, with the most distinct entities parapatric (but altitudinally separated) along the eastern edge of the Rocky Mountains.

Introduction

In 1974 I collected a series of *Lycaena* from northern California which seemed intermediate between *xanthoides xanthoides* and *x. editha.* In attempting to place this series I found that an error has been perpetuated in the systematics of the group. I will attempt to show that *xanthoides* and *x. editha*, previously considered separate species, are closely related and connected by intermediate populations, and that *x. dione,* previously treated as a subspecies of *xanthoides,* is much more distantly related.

Characters studied include male and female genitalia, the eleven wing pattern characters listed and described in the explanation for Fig. 1, the position of the submarginal brown spot in cell $Sc+R_1$ on ventral hindwing, forewing shape, and the uniformity (solid versus lighter centers) of ventral hindwing median and basal spots.

Results

Genitalia. 54 dissections of male and female genitalia were made of all entities of the group, but the only difference found was a general increase in robustness of genitalia as size increases from *"montana"* to *editha* to intermediate populations to *xanthoides* to *dione.* Valvae and sterigmae are too variable individually to detect differences, and the valval process usually differs as much between right and left valvae as between individuals.

Wing pattern. Fig. 1 plots most wing characters. The *x. dione, x. editha,* and *x. "montana"* samples are from several locations each, which were combined in Fig. 1 when found to have the same wing pattern.

The series from Dunsmuir in northern California is intermediate between *x. editha* and *x. xanthoides* in every trait by which the two are distinguished: in wing length, in size of ventral hindwing spots, and in thickness of submarginal white band on ventral hindwing (this character is of little value because it varies somewhat between *x. xanthoides* populations). The Dunsmuir series has a slightly less well developed red marginal band on dorsal hindwing, a character which does not differ appreciably between *x. editha* and *x. xanthoides.*

The series from near Mather on the western slope of the Sierra Nevada in central California, is also intermediate between *x. xanthoides* and *x. editha* (Fig. 1). It is intermediate in wing length, and is also intermediate in ventral hindwing postmedian spot size except that the maritime Point Richmond *x. xanthoides* population approaches it in spot size. The submarginal white band on ventral hindwing is thicker than in most *x. xanthoides* populations. The smallest and most heavily spotted male from near Mather (collected September 4) was reported as *editha* by Shields (1966), who reported the other intermediate specimens (collected 24 June to 1 August) as *xanthoides.* The very late September date of the former specimen may mean that it flew down from higher altitude in Yosemite Park to the east, where numerous *x. editha* populations occur.

The previous classification, which grouped *x. xanthoides* and *x. dione* into *xanthoides,* and *x. editha* and *x. "montana"* into another species *(editha),* is wrong because *x. editha* and *x. xanthoides* are much more similar to each other than either is to *x. dione. L. x. xanthoides* and *x. editha* differ basically by only two characters. *L. x. dione* differs from *x. editha* and *x. xanthoides* in eight characters: it 1) has more black spots on margin of ventral hindwing, 2) has more red lunules there, 3) has more red lunules on margin of ventral forewing, 4) has the red band on margin of dorsal hindwing slightly better developed and thicker, 5) and has a whiter ground color of ventral hind wing. 6) The submarginal ventral hindwing brown spot in cell $Sc+R_1$ seems to be closer to wing base than the same spot in cell Rs in *x. dione,* but is usually equal to or farther from base in *x. xanthoides* and *x. editha.* 7) The ventral hind wing median and basal spots have lighter centers in *x. xanthoides* and *x. editha,* but are solid black in *x. dione.* 8) The male forewings seem more rounded in *dione* than in the others.

L. x. "montana" differs slightly from *x. editha* in having slightly smaller wing length, slightly larger ventral postmedian spots, slightly fewer black spots and red lunules on margin on ventral hindwing, and slightly greater extent of red on margin of dorsal fore- (females) and hindwing and of orangish flush on female dorsal forewing.

The three *x. xanthoides* samples differ somewhat from each other. The Point Richmond sample was collected within 100 meters of the sea of San Francisco Bay, and differs in several traits from inland samples: it is somewhat larger, has slightly larger postmedian spots on ventral hindwing, has a somewhat thinner white submarginal band on ventral hindwing (like *x. dione*), has a somewhat browner ventral ground color, and has slightly greater orange flush on ventral forewing. It is slightly more similar to *x. editha* than are the other two *x. xanthoides* samples. The few inland northern California samples examined appear more similar to southern California populations.

Except for local trends, the geographic variation within this group shows a cline from *x. "montana"*, to *x. editha,* to the California populations intermediate between *x. editha* and *x. xanthoides,* to *x. xanthoides,* and finally to *x. dione.* A roughly clinal pattern is shown by these characters: wing length, width of postmedian-median ventral hindwing spots, number of red lunules and width of white band on ventral hindwing margin, color of ventral hindwing, and number of red lunules on margin of ventral forewing. The two most different members are *x. "montana"* and *x. dione,* and the major gap in the cline is that between *x. xanthoides* and *x. dione. L. x. xanthoides* and *x. dione* are separated by almost 2000 km at present, although I think that in Pleistocene or earlier time intermediate populations probably occupied Arizona, New Mexico, or Mexico. The cline is therefore horseshoe-shaped, and the two endpoints are now parapatric but altitudinally separated from Colorado to Montana.

Distribution (county records only for the U.S.) *L. x. editha.* ALBERTA: southern foothills, Calgary-McLeod area; COLORADO: Moffat, Routt, Grand, Gilpin, Jackson, Larimer; WYOMING: Sheridan, Park, Bighorn, Johnson, Teton, Sublette, Fremont, Lincoln, Converse, Platte, Albany, Yellowstone Nat. Park; MONTANA: Ravalli, Flathead, Missoula, Granite, Lewis & Clark, Cascade, Chouteau, Jefferson, Gallatin, Sweetgrass, Beaverhead, Madison, Carbon, Lake, Stillwater, Mineral, Broadwater; IDAHO: Clearwater, Shoshone, Adams, Latah, Idaho, Lemhi, Fremont, Custer, Clark, Bear Lake, Valley, Boise, Ada, Elmore, Blaine, Cassia; UTAH: Salt Lake, Summit, Cache, Rich; NEVADA: Elko, Washoe, Storey, Ormsby; WASHINGTON: Walla Walla, Columbia; OREGON: Klamath, Morrow, Crook, Umatilla, Wallowa, Union, Baker, Wheeler, Grant, Lake, Lane, Harney, Jackson; CALIFORNIA: Siskiyou, Shasta, Plumas, Sierra, Tehama, Tuolumne, Madera, Inyo, Alpine, Nevada, Placer, Mariposa, Modoc, Mono, Tulare.

L. x. xanthoides. OREGON: Benton, Jackson, Yamhill; CALIFORNIA: San Diego, Los Angeles, Kern, Inyo, Riverside, Mendocino, Orange, Monterey, Tulare, Contra Costa, Lake, Marin, Stainislaus, Santa Clara, Alameda, Tuolumne, Sonoma, Solano, San Mateo. BAJA CALIFORNIA NORTE: just south of Calif.

L. x. dione. COLORADO: Larimer, Weld, Morgan, Logan, Sedgwick, Phillips, Yuma, Boulder, Jefferson, Denver, Adams, Arapahoe, Douglas, Elbert, El Paso, Fremont, Pueblo, Kit Carson, Bent, Prowers; WYOMING: Campbell, Bighorn, Sheridan, Johnson, Crook, Converse, Platte, Albany; MONTANA: Glacier, Prairie, Custer, Lewis & Clark, Sweetgrass, Cascade, Chouteau, Stillwater, Carbon; NORTH DAKOTA: Bottineau, Cass, Grand Forks, McKenzie, Pembina, Slope; SOUTH DAKOTA: Lawrence, Codington, Harding, (Marshall or Roberts); NEBRASKA: Dawes, Sheridan, Deuel, Platte, Dodge, Kearney, Adams, Fillmore, Douglas, Saunders, Seward, Lancaster, Nuckolls, Thayer, Jefferson, Gage, Johnson, Nemaha, Pawnee, Richardson, Saunders; KANSAS: Scott, Riley, Johnson, Pottawatomie, Greenwood, Douglas, Franklin, Marion; OKLAHOMA: Rogers, Cleveland, Craig; MISSOURI: Jasper, Randolph, Johnson, Cass, St. Clair, Clay, Morgan, Carroll, Livingston, Lafayette, Buchanan, Saline, Jackson, St. Charles, Holt, Vernon; IOWA: Guthrie, Story, Linn, Pottawattamie, Johnson, Woodbury, Winneshiek; MINNESOTA: Hennepin, Rock, Houston, Wabasha, Polk, Aitken, Big Stone, Winona, Pipestone, Redwood, Goodhue, Scott, Dakota, Lac Qui Parle, Kanabec, Clay, Lake, Sherburne, Carlton; WISCONSIN: Grant, Eau Claire, Milwaukee, Marquette, Burnett, Dane, Door, Pepin, Chippewa, St. Croix; ILLINOIS: Mercer, Madison, Henderson, McDonough, Pike, McLean, LaSalle, Kane, Lake, Cook, DuPage, Grundy, Putnam, Marshall, Peoria, Livingston, Ford, Champaign, Shelby, Cass; MANITOBA: Victoria Beach, Winnipeg, Silver Height, Brandon, Housavick, Rosebank, Beulah, Birtle, Miniota, near Transcona; SASKATCHEWAN: Punnichy, Saskatoon, Lloydiminster, Tantallon, Fort Qu'Appelle; ALBERTA: Johnson Creek near Plateau Mtn., vic. Medicine Hat, Lethbridge, Calgary, Wainwright, Edmonton, Crows Nest Pass, Tilley, head of Pine Creek, Waterton area.

Interdigitation of ranges. L. x. editha occurs at higher altitude than *x. xanthoides* and *x. dione,* so that in some cases *x. editha* and one of the other subspecies occur near each other in mountains versus lowlands. *L. x. editha* and *x. dione* occur in the same county in Montana (2 counties), Wyoming (5 counties), and Colorado (1 co.), but never occur together at the same locality, because of altitudinal separation. *L. x. xanthoides* and *L. x. editha* are also altitudinally separated where their ranges interdigitate in southern Oregon and California (both occur in Jackson Co. Ore.). In northern California *x. xanthoides* occurs below 1000', whereas in the southern Sierra Nevada it occurs at higher altitudes.

Immatures. No differences between the species other than size have been found among eggs, larvae, or pupae as yet. *L. x. dione* eggs are larger with coarser sculpturing than eggs of *x. editha.* Comstock & Dammers (1935) found that *x. xanthoides* larvae are quite variable in color, and Skinner (1893) found no obvious difference between larvae of *x. dione* and *L. hyllus* (Cramer).

Hostplants. It has been thought that *x. xanthoides* larvae eat *Rumex,* whereas *x. editha* larvae eat *Potentilla.* However, the *Potentilla* records for *x. editha* are dubious; it also eats *Rumex. L. x. xanthoides* hosts include *Rumex hymenosepalus* (Comstock & Dammers 1935), *Rumex* sp. (Scott & Opler 1974, reported erroneously as *R. hymenosepalus*), *R. pulcher* (Emmel & Emmel 1973), *R. crispus* and *R. californicus* (both larvae reared, Idyllwild, Riverside Co. Calif., John F. Emmel, pers. comm.), and both *R. crispus* and *R. conglomeratus* (Shapiro 1974). *Hemizonia* sp. (Tietz 1972) is an error because it is not listed in either of te sources Tietz cites. *L. x. dione* hosts include *Rumex obtusifolius* (Forbes 1960; Leussler 1938-1939), *R. salicifolius triangulivalvis* (ovipositions Red Rocks, Jefferson Co. Colo., 12 July 1973, J. Scott), *R. occidentalis* (oviposition 2 mi. N. Idledale, Jefferson Co. Colo., 1977, J. Scott), *R. crispus* (oviposition 2 mi. N. Idledale, 1977, J. Scott), *R. "longifolius"* (Skinner 1893; Tietz 1972 cites this record under the name *R. occidentalis*), and "blunt-leaved dock" (Hooper 1973). *L. x. editha* hosts include *Rumex acetosella* (ovipositions Toll Ranch, Gilpin Co. Colorado, 27 July 1977, J. Scott; oviposition Jim Creek, Grand Co. Colo., 9 August 1977, J. Scott; oviposition California, Emmel & Emmel 1974), *R. gracilescens* (Tilden 1959), *R. paucifolius* (Garth & Tilden 1963), *Polygonum phytolaccoides* (oviposition Donner Pass, California, A. Shapiro pers. comm.). Both *Rumex* and *Polygonum* are Polygonaceae. Records of *Potentilla (Horkelia) fusca* (oviposition on leaves, Lembert 1894) and *Potentilla tenuiloba* (Comstock 1927) are old and somewhat dubious in view of the behavior of females in crawling down a hostplant stem and laying eggs haphazardly on or near stems or trash nearby.

Discussion

I treat *L. x. xanthoides* and *x. editha* as conspecific because: 1) they differ only by two wing characters (one or both of which might be influenced by temperature); 2) the Dunsmuir and Mather populations which are intermediate, indicating the probability of gene flow between the two; and 3) they both use Polygonaceae as larval hosts. *L. x. dione* could be considered a separate species because it is the most distinct entity, but I treat it as a subspecies of *xanthoides* because previous authors have done so (Clench 1961) and because it forms one end of a cline involving the other entities. The Rocky Mountain *x. "montana"* differs slightly from *x. editha* as noted above, and forms the other end of the cline. Because *"montana"* is less distinct than the other three entities I prefer to treat it as a synonym until more complete studies of geographic variation are made of *L. x. xanthoides* and *x. editha.* Some persons may wish to consider *"montana"* a valid subspecies. *L. x. "luctuosa"* Wats. & W. P. Comstock, named from Tehachapi, California, I treat as a synonym of *xanthoides* for the same reason. The name *luctuosa* may be useful when the geographic variation within *x. xanthoides* is better studied and a specific type locality for *xanthoides* is designated. The following treatment is suggested.

L. xanthoides
  a. *x. dione* Scudder 1868
  b. *x. xanthoides* (Boisduval) 1852
    luctuosa (Watson & W. P. Comstock) 1920
  c. *x. editha* (Mead) 1878
    montona Field 1936

It would be of great interest to know the effect of temperature on the wing pattern of *xanthoides.* The smaller and more heavily spotted *x. editha* might result partly from its higher altitude environment when compared to lowland *x. xanthoides.* The maritime Point Richmond *x. xanthoides* might be influenced by climate as well. Other California butterflies such as *Phyciodes campestris* are known to differ with altitude in part due to environmental causes (A. Shapiro pers. comm.).

It is of interest that Johnson & Balogh (1977) in describing *L. rubidus ferrisi* as a distinct species, justified this in part by stating that the differences between *L. rubidus* (Behr) and *L. r. ferrisi* are as great as those between *x. xanthoides* and *x. editha.* This paper shows that the comparison can no longer be used as justification. I dissected a series of *r. ferrisi* collected by Kilian Roever and found very little difference between it and *rubidus* (or *xanthoides*) in either male or female genitalia. The valvae are variable and very similar although *r. ferrisi* has slightly shorter valvae which can be seen only by using measurements or by placing the two side-by-side. Several wing pattern differences were noted, although one *r. ferrisi* lacks the ventral forewing orange flush considered diagnostic, and other *r. ferrisi* have the wing shape of *rubidus* rather than the shorter wing shape considered diagnostic of *r. ferrisi.*

Three apparent interspecific hybrid *Lycaena* were found during this study and indicate that mating occurs successfully between entities more different than are the subspecies of *xanthoides* or *rubidus.* David Wagner caught an apparent F_1 hybrid between *L. x. dione* and *L. rubidus* in the foothills west of Fort Collins, Larimer Co. Colorado. Marc Epstein caught an apparent F_1 hybrid between *L. x. editha* and

L. rubidus at Rabbit Ears Pass, Routt Co. Colorado. The Los Angeles County Museum has a female from Castella, Shasta Co. California, July 1903 (J. A. Comstock collection) in which the underside resembles a very heavily marked *L. heteronea gravenotata* Klots but the upperside resembles a partly orange female *L. rubidus* (*heteronea* females lack orange). Considering that *rubidus* does not occur in the area (except for one dubious specimen labeled "Mt. Shasta"), and that *heteronea* occurs there only as ssp. *L. h. heteronea* Boisduval, it probably represents a hybrid between *L. h. heteronea* and another *Lycaena,* possibly an *L. xanthoides* intermediate population like at Dunsmuir only a few km to the north, or *L. nivalis* (Boisduval).

One female from Point Richmond has 6 large submarginal blue spots on each wing. This is significant in showing that the ability to produce blue (which reflects ultraviolet) is present in the gene pool of this species, which is otherwise nonreflective in uv. Ultraviolet reflection is frequent in other *Lycaena* (Scott 1973). Orange flush on ventral forewing was not found in *x. dione* in this study although Clench (1961) states that occasional individuals have it.

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Appendix

Localities and Characters Studied: The sample of *x. dione* is from Colorado (21), Iowa (3), Alberta (1), Missouri (6, coll. R. Heitzman); others from Colorado (60) and Iowa (1) were examined but not included in Fig. 1. *L. x. xanthoides* are from San Diego Co. California (29, coll. O. Shields and R. Breedlove), near Techachapi, Kern Co. California (2), Glacier Lodge, Inyo Co. Calif. (1, coll. C. L. Hogue), Havilah, Kern Co. Calif. (1, coll. O. E. Sette), Greenhorn Mts., Kern Co. Calif. (2, M. L. Walton), Big Pine Meadow, Tulare Co. California (15), Point Richmond, Contra Costa Co. Calif. (28). Others from northern California (12) and Point Richmond (114) were examined but not included in Fig. 1. *L. x. xanthoides-editha* intermediates are from Railroad Park, 2250 ft., Dunsmuir, Siskiyou Co. California, 23 June 1974 (17), and from the vicinity of Mather (most 1 mi. east), Tuolumne Co. Calif. (20, coll. O. Shields), about 4600 ft. *L. x. editha* from Klamath Co. Ore. (5), Siskiyou Co. Calif. (4), Shasta Co. Calif. (9), Plumas Co. Calif. (9), Sierra Co. Calif. (1), Tehama Co. Calif. (1), Tuolumne Co. Caif. (2), Madera Co. Calif. (3), all coll. by O. Shields, D. Dirks, T. Preston Webster. 148 others from Inyo, Placer, Modoc, Tehama, Siskiyou, Shasta, Mono, Alpine, Tuolumne, and Nevada Cos. California, and Wallowa, Crook, and Klamath Cos. Oregon, were examined but not included in Fig. 1. *L. x. "montana"* are from Ravalli Co. Mont. (7), Cascade Co. Mont. (4), Sheridan Co. Wyo. (3), Yellowstone Park Wyo. (3), Moffat Co. Colo. (4), Routt Co. Colo (1), Grand Co. Colo (14), Gilpin Co. Colo. (13). Most were collected by myself unless otherwise noted. Some are from the Los Angeles County Museum.

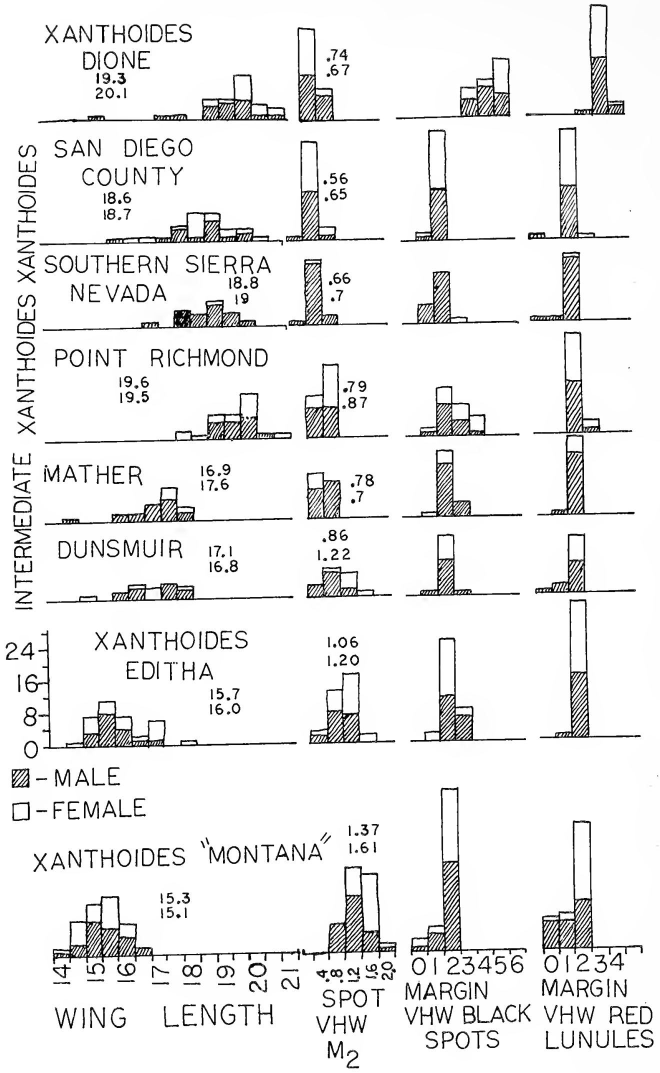
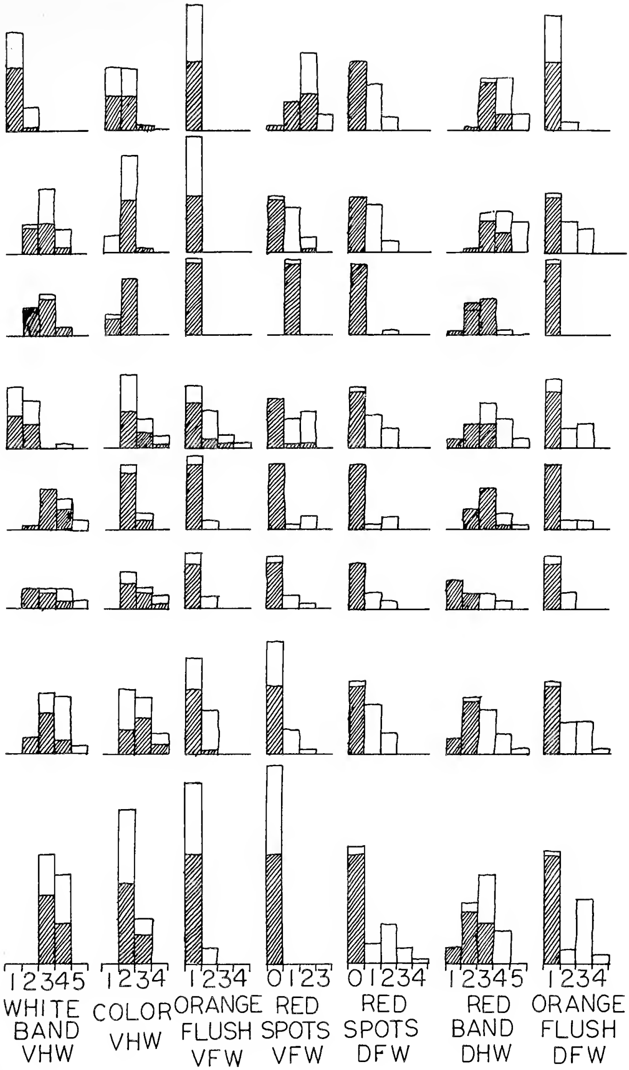


Fig. 1 Histograms showing the number of individuals of each sex which have each character state. Character states are (characters from left to right): 1) length of right forewing (mm); 2) width (mm) parallel to wing veins of ventral hindwing postmedian brown spot in cell M_2 (in intervals of .4 mm starting with 0, .4, .8, 1.2, 1.6, 2.0); 3) number of spots on margin of ventral hindwing which are black rather than brown (from 0 to 6); 4) number of red lunules on margin of ventral hindwing (from 0 to 5); 5) thickness of submarginal white band capping the marginal spots on ventral hindwing (1-very thin, about .3 mm thick; 2-thin, about .5 mm thick; 3-thicker, about .8 mm thick; 4-thick, about 1.2 mm thick; 5-very thick, more than 1.5



mm thick); 6) ground color of ventral hind wing (1-whitish gray; 2-whitish tan; 3-tan; 4-light brown); 7) degree of orange flush on disc of ventral forewing (1-no orange or ochre flush; 2-ochre flush; 3-orange-ochre; 4-mostly orange); 8) number of red lunules on ventral forewing margin (from 0 to 3); 9) number of red spots on dorsal forewing margin (red spot in cell 2A not counted) (from 0 to 4); 10) extent and thickness of dorsal hindwing marginal reddish band (1-absent; 2-only a few thin lunules; 3-longer but thin; 4-long and thick; 5-long and very thick); 11) extent of orange-ochre flush on dorsal forewing (1-absent; 2-several spots; 3-about 6 spots; 4-half of wing orange-ochre). Means for the first two characters are given (male mean above, female mean below).

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A New Species of *Coloradia* in California (Saturniidae, Hemileucinae)

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Abstract. *Coloradia velda, sp. nov.,* is shown to be an undescribed species inhabiting the San Bernardino Mountains, San Bernardino County, California, based upon a series of 50 specimens. These were compared with specimens of *Coloradia pandora lindseyi* and *Coloradia pandora davisi, Coloradia doris, Coloradia luski,* and *Coloradia euphrosyne*. The genitalia of *Coloradia velda* are unique in their structure among the five known species of *Coloradia* in North America. Its genitalia were compared with specimens of genitalia from *Coloradia doris* and *Coloradia luski,* and with the genitalia figures of *Coloradia pandora* subspecies, and that of *Coloradia euphrosyne* figured by Ferguson, 1971. The moth flies generally through the pine woodlands above 1400 meters late at night in June, with greatest abundance in pure stand Pinyon Pine woodland of *Pinus monophylla.*

Introduction

For a number of years, mostly in June, we have taken specimens of a *Coloradia* in the San Bernardino Mountains, San Bernardino County, California. Ferguson (1971) figures a specimen on Plate 11, Figure 8, taken by Grace and John Sperry at Barton Flats, June 1, 1946. Mr. Lance Dunmire, a former student of Johnson, took one male in 1971 at Seven Oaks, as has Erich Walter. Erich Walter took his first specimen at Crab Creek crossing near Crab Flat Forest Service Campground on the night of July 27, 1963. Later, Walter, accompanied by Mr. Kenneth Denton of Laguna Beach, found the species at Coxie Meadow. The authors have collected additional specimens at Horse Spring Campground. Mr. Charles Bellamy took a female at Cactus Flat along Highway 18, and Robert Velten took a male at Barton Flats Forest Service Campground. It is evident that the species has a wide distribution through the San Bernardino Range.

The writers have compared these specimens with a male *Coloradia doris* Barnes (1900) taken at light June 24, 1968, and two male *Coloradia luski* Barnes and Benjamin (1926) taken at light June 24, 1968, and July 4, 1969, by John R. Johnson, at Indian Writings Camp in North Ponil Canyon of the Philmont Scout Ranch in the Sangre de Cristo Mountains at an elevation of 2000 meters and sixteen kilometers northwest of Cimarron, Colfax County, New Mexico. Genitalia were prepared from one specimen of each of these species for comparison with the San Bernardino taxon. The San Bernardino specimens also were compared with specimens *Coloradia pandora lindseyi* Barnes and Benjamin (1926), *Coloradia davisi* Barnes and Benjamin (1926), and *Coloradia euphrosyne* Dyar (1912), as well as with the figures of *Coloradia* species provided by Ferguson (1971), and with his description of the type of *C. euphrosyne* as well as with that of Dyar's original description. It is very evident that the San Bernardino taxon is unique both in appearance and in its genitalia in comparison with all other known species of *Coloradia* of North America. See Figures 1 and 2. It is unfortunate that the specimen collected by the Sperrys, the only specimen to be figured in color by Ferguson (1971), is very atypical in its appearance. Of the fifty specimens we have before us, only one approaches it in appearance.

Coloradia velda Johnson and Walter **species novum**

Male: Thorax and abdomen robust. Dorsum of the thorax with dense, long, white-tipped, black hair-like setae. First abdominal segment white, second commonly black, remaining segments with white-tipped long setae, forming a fringe on the lower sides. **UPF**: Scaling more dense than in *doris* and *luski*, resulting in greater opacity of the wings. Majority of *velda* males have markings bright, contrasting, and well-defined. Basal area with conspicuous tuft of long, bright pink setae at proximal ends of anal veins. In many specimens pink setae and scales are scattered along the fringe of the anal margin to the anal angle where an evident pink edge is developed. Antemedial line strong, black, edged on the distal side with white, the white forming a conspicuous patch at the costal margin, the line with a prominent tooth projecting into the cell. Discal spot roundish to square, black, with a few white scales usually present at the center, the spot about equidistant from the ante- and postmedial lines. Postmedian line strong, black, toothed at the veins, and accented with white on the proximal edge. Median and submarginal areas peppered with white scales. Submarginal area variable in the development of the markings. In most specimens at the apical angle three black lunules are present between the branches of the radius, accented distally by white scaling that continues down the submarginal area in a sinuous, interrupted line or band to the anal angle, the line being toothed at the veins. Fringes at the outer margin are black with points of white scales at vein ends. **UPH**: Scaling heavy, reducing translucence of the wings. Wing patterns strongly marked. From the base to the discal spot wing is clothed by long bright pink setae and scales, continuing along the second anal vein and anal margin to the anal angle, forming a rich, copious pink fringe on the wing margin. Discal spot a narrow black bar. Distad of discal spot outer wing well-scaled in black, crossed by a curving band of pale pink midway between discal spot and outer margin, extending from costal to anal margins. Distad of the pale pink band the submarginal area dusted with pale pink scales between veins. Fringes of the outer margin black with points of pale pink scales at the vein ends. UNF: Basal area and costal margin strongly pink, the median area shading into black caudad of the solid black discal spot. Postmedial black band strong, margined on distal edge by a pink band. Three black lunules between radial veins at apex, submarginal area black, dusted with pink scales. **UNH**: Based of discal spot and along second anal vein and anal margin pink, paler than UPS. Costal margin white to pink scaled from base to intersection with postmedial band. Discal spot black. Wing distad from discal spot black-scaled to outer margin, black scaling forming a well-defined postmedial band continuous with that of the primaries and originating at the costa from a somewhat rectangular spot of dense black scaling. Postmedial band bounded on distal edge by a band of pale pink. Wing surface along the outer margin dusted with pink scales.

Female: Larger than the male; *C. velda* females more robust than those of *C. doris* and *C. luski.* In coloration *C. velda* females resemble males. UPF heavily scaled and opaque, the patterns varying in intensity and contrast in different individuals. Discal spots of the FW tend to be smaller and solid black in the females. The resemblances between sexes hold for both UPS and UNS. UPH much like males, well-scaled and opaque. UPS pink from base to or beyond discal spot and along the second anal vein and anal margin. Discal spot is larger than in the male, oval and black. Postmedial black well-developed from the costal to anal margins, bordered distally by a pale pink band. Wing surface along the outer margin black, dusted with pale pink scales between the veins. UNH much as the male, but with black costal margins.

Wing Expanse: Males -- 25.5-32.5 mm, mean 28.1, N = 28, holotype 30.0. Females -- 32.0-39.0 mm, mean 34.8, N = 20 allotype 37.0.

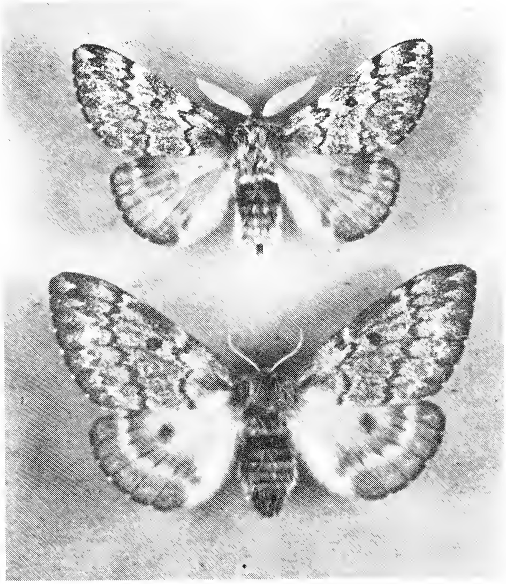


Figure 1. Types of *Coloradia velda.* Upper specimen, holotype male. Lower specimen, allotype female.

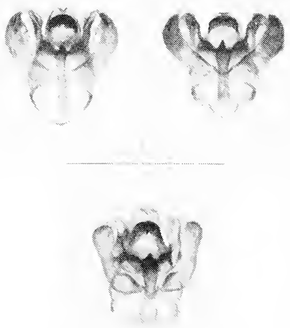
Types

Holotype. male. California, San Bernardino County, Coxie Meadow, 1700 M. 1 VII 1972 at UV light, E. and V. Walters. *Allotype.* as male except 15 VI 1972. *Paratypes.* All California, San Bernardino Co. at UV light. Coxie Meadow; 1700 M.; 2 ♀, 2 ♂, 1 VII 1965 (Kenneth Denton); 1 ♀, 2 ♂, 1 VII 1965 (E. Walters), 4 ♀, 2 ♂, 25 VI 1970 (J. W. Johnson); 3 ♀, 1 ♂, 25 VI 1970 (W. Walters); 2 ♀, 1 ♂, 6 VI 1972 (E. Walters); 1 ♀, 2 ♂, 15 VI 1972 (E. Walters); 4 ♀, 5 ♂, 14 VI 1974 (E. Walters); 1 ♀, 19 VI 1974; 5 ♀, 5 ♂, 6 VI 1975 (J. W. Johnson); 4 ♀, 6 VI 1975 (E. Walters); 1 ♀, 19 V 1976 (J. W. Johnson). Cactus Flat Hwy. 8 12.8 km north Big Bear, 1800 M., 1 ♂, 15 VI 1974 (Charles Bellamy). Barton Flats Campground, 2000 M., 1 ♀, no date (Robert Velten); 1 ♀, 1 ♂, 6-7 VI 1955 (J. A. Comstock). San Gorgonio Public Camp, Mill Creek, 1646 M., no date (G. R. Noonan), Doble, 2255 M, 6 ♀, 28 IV 1959 (Chris Henne) (these are bred specimens presumably eclosed at a much earlier time of year than would be expected in the natural habitat). Hanna Flats, 2064 M., 1 ♀, 1 IV 1954 (Arnold Menke) eclosed after two years in pupa.

Type Disposition: Holotype will remain in the collection of Walter, but pledged to Los Angeles County Museum of Natural History (LACMNH) with an unspecified number of paratypes. Allotype and remained to paratypes to remain in the Walter Collection. J. W. Johnson paratypes, one pair each to the LACMNH and the USNM, remainder in the Johnson Collection. The Denton paratypes to remain in the Denton Collection, Univeristy of California at Irvine. The Bellamy and Velten paratypes in the collection of Lawrence Shaw. Remainder in the LACMNH collection.

Discussion

Coloradia velda differs from both *C. doris* and *C. luski* in its greater size and robustness, in the wider, more angular primaries, in the greater intensity of scaling reducing the translucency of the wings so evident in the other two species. *C. velda* also has a bright, strongly developed, and contrasting pattern on both primaries and secondaries, differing in this respect not only from *doris* and *luski*, but also from *euphrosyne*. Through the courtesy of Dr. E. E. Sleeper, California State University at Long Beach, and Mr. Lawrence H. Shaw, opportunity was afforded of directly comparing *C. velda* with three male specimens of *C. euphrosyne* collected by Dr. Sleeper July 14 and 15, 1979, in the State of Michoacan, Mexico, 280 kilometers east and 0.8 kilometers south of Morelia. These specimens are strikingly different from *C. velda.* Two of the males were very similar to the description of the type of *C.*



Figures 2-4. Genitalia of three *Coloradia* taxa, ventral view. X 18.
Fig. 2. *Coloradia luski.*
Fig. 3. *Coloradia doris.*
Fig. 4. *Coloradia velda.* Compare the shapes of the valves, penes, transtilla alary processes, and the tergal plates dorsal to the uncus in the three species. The *C. luski* and *C. doris* genitalia prepared by Dr. R. H. T. Mattoni. The *C. velda* genitalia and all micrographs by J. W. Johnson.

euphrosyne given by Ferguson (1971, pp 100-101). The third male was lighter in general coloration. The patterns of the primaries of *C. euphrosyne* are indistinct, the antemedial line much like that of *C. luski*, but of low contrast, and the postmedial band close to the discal spot. The secondaries are almost wholly bright pink or red with a large black discal spot and black border. The inferior surfaces were almost wholly red. The *C. velda* was compared with a *Coloradia pandora davisi* of the California State University at Long Beach through the courtesy of Dr. Sleeper and Mr. Shaw, the specimen having been taken on Mount San Pedro Martir 320 kilometers south of the California border in Baja California, Mexico. *C. velda* was compared finally with *Coloradia pandora lindseyi* taken by the authors in the San Bernardino Mountains. There is little resemblence between *C. p. davisi* and *C. p. lindseyi* and *Coloradia velda.*

Genitalia: in *luski* the penis is long and slender, the valves crescentic and pointed, and the tergal plate covering the uncus exceeding the uncus significantly and strongly emarginate. In *doris* the penis is shorter and wider, the valves crescentic and pointed, and the tergal plate over the uncus scarcely exceeding the uncus and scarcely emarginate. In *velda* the penis is long and wide, the valves narrow and parallel-sided with bulbous rounded ends. In all three species the transtilla has a median black sclerotized spine with alary processes extending laterally and dorsally between the valves and uncus, the shapes of these processes differing in each species. In *C. velda* the transtilla alary processes are very similar to the valves, parallel-sided and rounded and bulbous on the tips. The tergal plate over the uncus well exceeds the uncus and is round and bulbous, much as in *C. euphrosyne*, but differently sculptured. *Coloradia velda* clearly is a distinct species from other known species of the Genus *Coloradia* in North America.

Although *Coloradia velda* has been taken in small numbers in the Jeffrey Pine, *Pinus jeffreyi*, forest of the higher southern reaches of the San Bernardino Mountains, the authors have found the densest populations in the high pure Pinyon Pine, *Pinus monophylla*, woodlands of the northern areas of the range. The authors have not recovered young stages from pinyon pine, but the occurrence of the species in woodland remote from other pine species suggests that pinyon pine may be the preferred food plant. At other sites where it has been taken pinyon pine can be shown to be present scattered through the forest of other coniferous species. The emergence of *Coloradia velda* peaks in June.

Acknowledgements: The authors express their thanks to Dr. Charles H. Hogue and Mr. Julian P. Donahue for assistance in the study of the paratypes of the Los Angeles County Museum of Natural History collections; to the gracious assistance of Dr. R. H. T. Mattoni for preparation of genitalia; to Mr. Lawrence H. Shaw for preparation of genitalia, and to Mr. Haw and Dr. E. L. Sleeper for making available specimens of *Coloradia euphrosyne* and *Coloradia pandora davisi* from the California State University at Long Beach collections; to Mr. Kenneth Denton for examination of his paratypes; and especially to Mr. Gordon Marsh, Director, Museum of Systematic Biology, University of California, Irvine, for his indispensable assistance in securing references through the University of California loan services.

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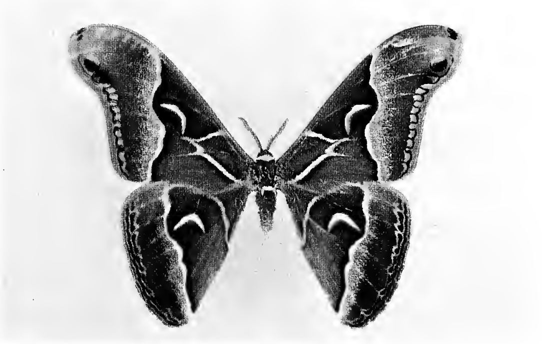

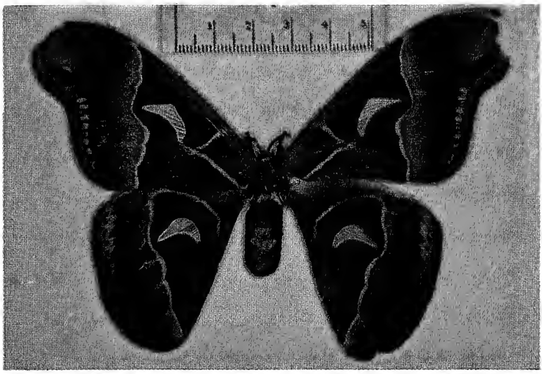

The color figure is to accompany a paper by LeMaire and Peigler which is in press *Nouvelle Revue d'Entomologie* 1981.

Samia watsoni Obertheur:

Fig. 3. Male from Kuatan, Fukien, China, collected 28 V 1938 by J. Klapperich.

Fig. 4. Male from West Tien-Mu Shan, Chekiang, China, collected 23 IV 1932 by H. Hone.

Fig. 5. Female from Omei Shan, Szechwan, China, reared from cocoon 30 IV 1922 by Rev. G. M. Franck.

Figs. 3 and 4 are of specimens in the Zoologisches Forschungsinstitut und Museum Alexander Konig, Bonn. Fig. 5 is in British Museum (Natural History).

Journal of Research on the Lepidoptera 18(1):68, 1979(80)

Book Review

The Butterflies of Oregon.
Ernst Dornfeld. 1980. Timber Press, P. O. Box 92, Forest Grove, Oregon 97116, 276 pp., 48 black & white plates, 4 color plates. 192 maps. $8^1/_2$ X 11 format, cloth. $24.95.

I started collecting butterflies when I was 12. What got me going was coming across Comstock's *Butterflies of California* in the public library. With the exception of all color plates, Dornfeld's book should similarly captivate kids of the Northwest. It offers a great deal more, too, in citing a substantial amount of bibliographic material and a set of distribution maps which alone justify the price. The book is a necessity for anyone with interests in the butterflies of the region, including general natural history oriented enthusiasts. The format and packaging are quite attractive. As with virtually all regional descriptive books, no one will be universally pleased. The introductory section of the book is most open to criticism, but the introduction must necessarily be brief. The sections on history and physiography of the state are good, relevant and interesting. The biology section is quite brief. In the systematics section the nature of variation and its corollaries in the species and subspecies concepts is rather simplistically covered without reference to the intellectual ferment going on in this exciting area (see Ehrlich & Raven, 1969. Science 165:1228; Ehrlich et.al., 1975. Science:221; and Bowden, 1979. Jr. Lep. Soc. 33:77). A brief mention is made on endangered species, which, with two exceptions, appears not a great concern in Oregon. The technique section is abbreviated, most unfortunately in the area of breeding, from which our greatest data deficiencies occur and in which the greatest encouragements should lie. The main point of the book is identification, and not classification and biology. Thus the more arcane contemporary points of controversy, as whether *Euphydryas chalcedona* and *anicia* are conspecific or *Euphilotes* is a subgenus of *Philotes* (it clearly is not), are not confronted. Such issues are, however, not the point of the book.

I am particularly gratified with the maps, and particularly that they depict actual localities using a dot system, and not cross hatching on shadowing, which do not convey nuances of distribution. For unknown reasons four blank maps are included for skippers which should be expected in the state. Only one map, for *Chlosyne leanira*, has its subspecies on a single map using different marks. it would have been more instructive to have done this for all the polytypic species rather than separate maps. Nonetheless, it is the maps which clearly point up interesting questions about morphological variation over space, particularly in indicating where one should look for populations which exhibit intermediacy and then trying to find out what significance the intermediacy demonstrates. In several cases the maps manage to question the whole idea of subspecies, e.g., *Speyeria zevene conchyliatus* and *S. z. picta/garretti*, and *S. egleis linda* and *S. e. dodgei* which overlap; the *Euphydryas anicia/chalcedona* complex and *E. editha colonia/remingtoni/lawrencei* situations which are quite intriguing from their map stories.

In summary, the virtues of the book outweigh its defects. Anyone with interest in the area should have it in their library.

R. H. T. Mattoni, 2130 So. Granville Avenue, Los Angeles, CA 90025.

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Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

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ON THE LEPIDOPTERA

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The Ecology and Biogeography of the Butterflies of the Trinity Alps and Mount Eddy, Northern California

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Abstract. The butterfly faunas of the Trinity Alps and Mount Eddy, northern California, were investigated during five field seasons in the hope that they would shed light on the biogeographic history of the high-elevation biota of the Sierra Nevada. In particular, relict plants are numerous in the region, and bear on various scenarios advanced by phytogeographers for range changes of plants in the Pleistocene. The Trinities and Mount Eddy are the only non-Sierran, non-volcanic mountains in northern California reaching subalpine and alpine heights.

The total Trinity-Eddy fauna includes 112 species. This fauna was compared with various Sierran faunas and with that of Crater Lake National Park, Oregon. Most of the subalpine - alpine fauna is differentiated at the subspecies level between the Sierra Nevada and the Trinity-Eddy region, and there are no known populations of taxa previously regarded as "Sierran endemic." Two subspecies are endemic to the Trinity-Eddy subalpine region. Several others extend into Oregon. One, limited to Deadfall Meadow and Deadfall Lakes, is disjunct from the central interior Oregon Cascades. The montane fauna is less differentiated than the subalpine.

Numerous differences in ecology and altitudinal distribution occur between the Trinity-Eddy region and northern Sierra. The Trinity-Eddy phenology is generally later, with a peak in abundance and diversity in autumn.

The Trinity-Eddy fauna offers no evidence contrary to either northern or eastern distributional routes into the Sierra, but is more strongly supportive of the former. Several possible explanations of the character of the fauna are discussed.

Introduction

The Trinity Alps, located about 80 km northwest of Redding, California, form a rugged and relatively inaccessible terrain including the highest peaks in the Klamath physiographic province. With extensive areas above 2100 m and a maximum elevation of 2744 m, the Trinities include considerable subalpine and limited amounts of alpine habitat situated roughly midway between the Pacific Ocean (about 100 km) and the Sierra Nevada - Cascade axis (about 115 km). This high country can be reached only on foot or horseback via the numerous trails in the Salmon - Trinity Alps Primitive Area, which is administered as wilderness by the U. S. Forest Service. To our knowledge the interior was visited only once by Lepidopterists before 1976. Yet the Trinity Alps are of great biogeographic and ecological interest for a number of reasons: they reproduce the complete set of altitudinal lfe zones characteristic of the west slope of the Sierra, but telescoped into a shorter and more abrupt elevational gradient; they receive exceptionally heavy precipitation which is seasonally more evenly distributed than in the high Sierra; they are an area of high botanical relictualism and endemism; they show abundant and dramatic evidence of Pleistocene glaciation; and they include an extraordinary edaphic diversity which is reflected in the vegetation up through the subalpine zone.

The fact that the Trinities provide potential habitats for the subalpine and alpine Sierran butterflies suggested their usefulness in testing a widely held (though not formally published) interpretation of the historical derivation of that fauna: that it came from the Rocky Mountains across the Great Basin in the Pleistocene. This is a familiar scenario in the literature of Sierran alpine botany (discussed further below). Because so few collectors had been into the Trinities, we quite literally had no idea what we would find. We determined to cover as many habitats as possible and over a period of several seasons. The Trinity Alps Project was inaugurated in June, 1976. By 1978 we realized that we would have to include Mount Eddy as the only potential "stepping stone" between the Trinities and the Sierra - Cascades. As our collecting progressed we became aware of the importance of the "arid" faunal component deriving from north and east of the mountains, and we made several forays down into Scott Valley. Ultimately the project involved 23 collectors for a total of over 200 man-days and over 700 km of trails and cross-country survey, resulting in an accumulation of over 5000 specimens of about 115 species, filling 17 Cornell drawers. At the end of August, 1979 the Pacific Slope Branch of the Lepidopterists' Society met at Davis and the meeting concluded with a field trp to the Eddies.

We are still not finished. In particular, the Deadfall Lakes and Mount Eddy have not been collected before July, so records of many spring species are missing from them. This hampers formal biogeographic analysis of the Eddies *vs.* the Trinities. The broad outlines of patterns have, however, emerged, and the data we know we are lacking are not of a sort likely to upset those patterns. We think it is now fair to say that the Trinities are better known Lepidopterologically than any area in the Sierra Nevada except the South Yuba River - Donner Pass region and Yosemite National Park.

Access to the Trinities requires a Wilderness Permit, which may be obtained at Redding, Mount Shasta City, Weaverville, or the Coffee Creek Ranger Station. Motorized vehicles are not permitted within the Primitive Area, or on Mount Eddy above Deadfall Meadow. Fire regulations are strictly enforced. We hope all Lepidopterists who may wish to visit this magnificent region will cooperate in preserving it in its primitive state for posterity.

The Trinities: The Physical Setting

Geography. -- The Klamath Mountains Province comprises an elongate, geologically complex area of approximately 30,560 km^2 in northwestern California and southwestern Oregon. Among the named ranges are the Trinity, Scott, Scott Bar, South Fork, Salmon, Trinity Alps, Marble and Siskiyou Mountains. The Trinity Alps are centrally located in the Province and are mapped on the following USGS 15′ topographic quadrangles: Helena, Trinity Lake, Coffee Creek, and Cecilville. Elevations range from 732 m near Trinity Alps Resort in the lower canyon of Stuart Fork to 2744 m at the summit of Thompson Peak, the highest point in the Province. The region is drained by the South Fork of the Salmon River and by the Trinity River, which has several major tributaries (North Fork, Stuart Fork, Canyon Creek, Coffee Creek) which head in the interior of the Alps. Most of the high country is contained in a circle of 13 km radius centered at 123°00′ W, 41°00′ N - an area of about 530 km^2. Approach is from California Highways 3 or 299. Many of the major trailheads are at or near Big Flat, on Coffee Creek Road which leaves Hwy. 3 northeast of Trinity Center. Other important trailheads are in the Stuart Fork and Canyon Creek drainages, respectively NNE and W of Weaverville. All the trails are shown on the Visitor's Map of the Trinity National Forest (North Half), available from the U. S. Forest Service. This map should be used in conjunction with the topographic quadrangles, as it is considerably more recent.

Climate. -- The climate of the Trinities is determined largely by westerly winds from the Pacific Ocean, and is of a montane - Mediterranean type modified by latitude and proximity to both the sea and the interior deserts of northeastern California and eastern Oregon. The only meteorological records made in the Alps proper are annual snow surveys compiled by the State Department of Water Resources. April readings for 1946 through 1967 indicate an average snow depth of 0.798 m with an average water content of 33.02 cm at Big Flat (1555 m), and 2.172 m and 97.54 cm on the south flank of Red Rock Mountain at 2013 m. Snow depths in the Caribou Basin are probably greater. In this very cold valley open to the north, frost may occur any night of the year and snow persisted at 2196 m into early August, 1976 in a year of below-normal snow pack. Midsummer high temperatures at 2100 - 2200 m range from 16 degrees - 27 degrees C in clear weather, with lows from 2 degrees - 10 degrees. Ferlatte (1974) states that the growing season at Big Flat "lasts from May to September" and is "proportionately shorter at higher elevations, probably limited to four or five weeks on the north side of Thompson Peak."

As is commonly the case in California, there are marked year-to-year variations in rain- and snowfall, growing season, and the timing of bad weather. Above 2200 m snowfall season is roughly mid-September through June. Because the Trinities are so far north, they are subject to frontal weather in summer which is uncharacteristic of the west slopes of the Sierra. Afternoon cumulus are of frequent occurrence and often mature into isolated thunderstorms. We, like all experienced Trinity campers, can testify to the violence of some of these storms, which may be accompanied by very cold downdrafts and hail. In some locations over 165 cm of orographic precipitation may fall in a year in the Trinities.

There are several "permanent" ice fields or glacierets in the Trinities, the most important of which (covering 2-2.5 ha each) are on the north side of Thompson Peak at 2500-2600 m. Smaller, semi-permanent ones occur elsewhere, as on the northwest side of Sawtooth Ridge, above the Caribou Basin. The persistence of this ice reflects both the heavy precipitation and sheltering in the shadows of the highest ridges.

Lithology. -- For their area, the Trinity Alps are extraordinarily complex (Irwin, 1960; Davis *et al.*, 1965). The three major rock types represented are pre-Jurassic metamorphics, Upper Jurassic - lower Cretaceous quartz diorites (granitics), and ultrabasics (ultramafics), mostly altered to serpentine. All of these exercise a great deal of control over soil and vegetation development.

The metamorphics are divided into three formations based on structural relationships and mineral composition: the Grouse Ridge Formation, consisting of micaceous quartzite, amphibolites, calc-shists, and impure marbles; the Salmon Formation of albite - epidote - hornblende schists; and the Stuart Fork Formation of metachert, micaceous quartzite, marbles, mica, greenstone and graphite phyllites. For the most part these rocks occur at low elevations, well within the montane zone; they reach their maximum elevation, and only penetration of the subalpine, at Packer's Peak (2387 m).

There are several bodies of granite in the Trinity Alps (Hotz, 1971). These are the Deadman Peak, Middle Fork, Canyon Creek, Caribou Mountain, Gibson Peak, Horseshoe Lake, Sugar Pine, Craggy Peak, and Russian Peak Plutons. The dominant plutonic rock is quartz diorite, but granodiorite occurs in the Russian Peak Pluton, north of the Alps proper. Most of the highest country is the Canyon Creek and Caribou Mountain Plutons. The distinctive landscapes of this country give the range its name and reputation for ruggedness.

Ultrabasics (ultramafics) occur only in the eastern half of the Alps, where they are the predominant rocks. They reach the subalpine level in a number of places, notably at Red Rock Mountain (2395 m) and throughout the Sunrise Creek - Landers Creek - Parker Creek - Union Creek area above 2100 m. The color of the ultrabasics - reflecting the mineralogy - varies greatly, from dull reds and ochres to blues and greens. The greatest local diversity occurs at Dorleska Summit (2135 m).

The contrasting colors and textures of Trinity rocks facilitate the tracing of glacial deposits to their sources (Sharp, 1960). They also facilitate correlation of vegetation types with soils. There are many dramatic contact zones, such as that between pre-Silurian metavolcanics (red) and quartz diorite - tonalite (white) (Caribou Mountain Pluton), which runs down Sawtooth Ridge and across Caribou Lakes.

The major valleys are filled with Quaternary glacial deposits and alluvium. Coffee Creek has huge piles of dredge tailings from gold mining operations earlier in this century. Both placer and hardrock mining were common. There are still some active gold claims in the region.

Structural History. -- In the late Jurassic (Lipman, 1962) the Alps were subjected to regional folding and metamorphosis and intruded by granitic and ultrabasic plutons. This period of tectonism and intrusion may be related to the formation of the ancestral Sierra Nevada. In late Cretaceous-early Tertiary time (MacGinitie, 1937) the landscape was worn down to a low relief, the so-called Klamath peneplain, with maximum elevations of 750-1500 m; the late Jurassic intrusives may have been first exposed at this time. Regional tectonism recommenced in the late Pliocene-early Pleistocene, with a westward tilting, resulting in highest elevations in the eastern part of the range (Irwin, 1960). Antecedent streams were rejuvenated and began cutting down the steep, narrow canyons characteristic of the lower elevations today. Much of the drainage in the Trinities is transverse to the trend of the mountains. Lipman (1962) discusses the effect of the plutons on the drainage pattern. The late Tertiary-early Quaternary uplift set the stage for the glaciation of the high country.

Glaciation. -- Sharp (1960) describes evidence for at least four substages of glacial activity in the Pleistocene Trinity Alps. Pleistocene histories in western North America are currently undergoing widespread re-evaluation in the light of the more complex chronologies derived from deep-sea sediment cores, and Sharp's scenario will probably need to be revised. He sees one stage as pre-Wisconsinian, perhaps as old as Kansan, with the others all being of Wisconsinian age. Sharp also feels that earlier glaciations may have occurred, as well as "neoglaciation" in the past 2000 years or less. He describes evidence for sheets of ice ("ice carapaces") 60-90 m thick, extending from the glaciers to the "schrund" lines below the ridge crests in the broad upper reaches of many of the valleys. "Bergschrunding" produced the steep cliffs, 15-90 m high, which are characteristic of the high granite country and make cross-country travel so difficult. Below them the canyon walls slope much less steeply down. The granite country has many classic glacial features, including striae and numerous cirques. In the ultrabasic country U-shaped valleys are well-developed (Sunrise, Parker, Union Creeks).

Moraines occur in all the major valleys, with debris flows below them in the valleys draining from ultrabasics. During the last ("Morris Meadow") glaciation the Alps contained at least 30 valley glaciers, extending down to about 1120 m; earlier stages had reached 750 m. Wisconsinian orographic snowline is interpreted as 1980 m, climatic snowline at 2440 m, as against modern values of 2290 m and 2745 m. Most of the present montane coniferous forest was probably subalpine during these maxima.

The Trinities: Vegetation

Ferlatte (1974) discusses the history of botanical studies in the Trinity Alps and attempts an ecological classification of plant formations there, recognizing five major zones. His book is a very valuable floristic reference but fails to convey much of an impression of the structure of plant communities or the degree of edaphic determinism in the vegetation. A regional survey of Klamath vegetation (Sawyer and Thornburgh, 1977) gives a coarse-grained impression of Trinity plant communities in a comparative context, and underscores the daphic influences. The material which follows is a composite from these sources and our own qualitative observations. The definitive work on Trinity vegetation has yet to be written.

Ferlatte recognizes the following zones:

Mixed Conifer Forest. - This is the lowest, described as "found on the valley bottoms and lower slopes of adjacent ridges" at 1550-1830 m. It is an ecotone between lower and higher-elevation species and includes Yellow Pine (*Pinus ponderosa*), Sugar Pine (*P. lambertiana*), Lodgepole Pine (*P. contorta* ssp. *latifolia*), White Fir (*Abies concolor*), Douglas Fir (*Pseudotsuga menziesii*), and Incense Cedar (*Calocedrus decurrens*). Understory species noted are *Viola sheltonii, Claytonia lanceolata* and *Lewisian nevadensis*, all spring species; *Orthocarpus copelandii* and *Haplopappus bloomeri*, fall species; also *Adenocaulon bicolor, Amelanchier pallida, Spiraea douglassii, Clintonia uniflora,* and *Pyrola picta*. This description seems predicated on the vicinity of Big Flat: "Snow has usually melted by early June, and different species can be found in flower from May to September."

Red Fir Forest. - Described as occupying "essentially a transition zone" with elevations of 1675-2135 m; "snow often remains until the end of June." Tree species are Jeffrey Pine (*Pinus jeffreyi*), Western White Pine (*P. monticola*), and Red Fir (*Abies magnifica* var. *shastensis*). Understory species include *Ribes nevadense, Leucothoe davisiae, Lupinus croceus, Veratrum viride*, and *Ligusticum californicum*.

Subalpine Forest. - Elevational range 2135-2595 m; "snow can last throughout the year in protected places;...occurs mainly along the summits of the higher ridges and in the higher basins." The trees listed are Foxtail Pine (*Pinus balfouriana*), Whitebark Pine (*P. albicaulis*), and Mountain Hemlock (*Tsuga mertensiana*). Associated species include *Arctostaphylos nevadensis, Anemone occidentalis, Kalmia polifolia* var. *microphylla, Phyllodoce empetriformis*, and *Cassiope mertensiana*.

Alpine Fell - Field. - This zone is said to occur on north-facing slopes above 2595 m, with a short growing season reaching its peak in mid-August. Characteristic species are listed as: *Saxifraga tolmiei, Sibbaldia procumbens, Ranunculus eschholtzii, Primula suffrutescens*, and *Oxyria digyna*. The type locality is the north side of Thompson Peak.

Montane Chaparral. - Reported by Ferlatte at 1550-2135 m on exposed, well-drained, gravelly slopes in the canyons of Coffee Creek, the South Fork of the Salmon River, and Canyon Creek. "Snow has melted by early May." Shrubby dominants are listed as *Quercus vacciniifolia, Ceanothus velutinus, Arctostaphylos patula*, and *Garrya fremontii*.

Sawyer and Thornburgh treat this classification as unduly simplified, and we agree. For one thing, the "zones" are by no means as distinct as Ferlatte's telegraphic generalizations imply - they really consist of complex mosaics of local communities along environmental gradients. Ferlatte's text also obscures the climatic gradient across the Trinities which reflects increasing continentality north- and eastward, and the rain shadow of the mountains themselves. Sawyer and Thornburgh have discussed this gradient and its effects on forest vegetation. We will limit ourselves to detailed discussion of non-forest (bog meadow) habitats of particular interest to butterflies and butterfly collectors, and to the subalpine and alpine zones, with emphasis on edaphic control of the vegetation. It should be understood that Ferlatte's *Flora* omits many species, including even some common ones like *Chrysothamnus nauseosus*; some of these are cited in our text. A revision of Ferlatte is in preparation (J. diTomaso, *pers. comm.*). The book is, however, essential for field work in the Alps.

The Bog Meadows. - Moist or wet meadows and bogs are frequent in the montane and subalpine Trinity Alps. Their vegetation has not been described in detail. They occur on both granitic and ultrabasic substrates, and their floras differ almost completely between the two.

The most extensive boggy areas on granitic substrates are in the Caribou Basin at about 2085 m. The herbaceous vegetation is extremely diverse. Some characteristic species are *Erigeron peregrinus* ssp. *callianthemus, Aster alpigenus* ssp. *andersonii, Ligusticum californicum, Anemone occidentalis, Gentiana newberryi, Allium validum, Lilium washingtonianum, Schoenolirion album, Veratrum viride, Habenaria sparsiflora, H. unalascensis, Listera convallarioides, Spiranthes romanzoffiana, Luzula parviflora, Carex spectabilis, Deschampsia atropurpurea*, and *Cystopteris fragilis*. Twinberry (*Lonicera conjugialis*) and several willows occur, but most characteristic are the Ericaceous shrubs forming a transition zone to adjacent

Mountain Hemlock forest: *Phyllodoce empetriformis, Vaccinium arbuscula,* and *Ledum glandulosum* var. *californicum.*

Only two conspicuous herbs which occur on granitic bogs also occur on ultrabasic ones: *Dodecatheon jeffreyi* and *Senecio triangularis.* Although granitic bogs are mostly on stream terraces and valley fills, ultrabasic bogs often occur on hillsides where semi-permanent seeps produce continually wet soils which support a distinctive plant community. This is related to what Hickman (1976) calls the *Caltha biflora - Carex sitchensis - Dodecatheon jeffreyi* community in the Oregon Cascades. The most characteristic plant of ultrabasic bogs in the Trinities is California Pitcher Plant (Cobra Plant), *Darlingtonia californica.* Ericaceous shrubs are completely absent. Some other characteristic species are: *Cirsium breweri, Helenium bigelovii, Raillardella pringlei, Lotus oblongifolius* var. *nevadensis, Dicentra pauciflora, Polygonum bistortoides, Caltha howellii, Gentiana calycosa, Trifolium longipes, Carex* spp. (*hassei, interior, jonesii, lemmonii, scopulorum, teneraeformis*), *Scirpus criniger* and *microcarpus, Agrostis alba,* and *Narthecium californicum.* Almost invariably the fringes of the bog, which dry in summer, are ringed by Bushy Cinquefoil (*Potentilla fruticosa*).

The serpentine seeps which run all summer make these habitats islands of green in a drying landscape. In September they turn a characteristic rusty color.

Subalpine and Alpine Vegetation. - The most characteristic subalpine tree on non-ultrabasics is *Pinus albicaulis.* It dominates in exposed sites on ridge crests, summits, and SW-facing slopes above 2200 m. Since this tree occurs to the virtual top of the Trinities, Sawyer and Thornburgh do not accept Ferlatte's claim of a climatic tree line. They attribute the "fell-fields" to poor soil development. *Tsuga mertensiana, Pinus monticola, P. contorta* and *P. jeffreyi* all occur in some stands. *T. mertensiana* forms almost pure stands in the Caribou Basin. *Polemonium pulcherrimum* and *Draba howellii* are two characteristic herbaceous components of the subalpine community.

On ultrabasics *Pinus balfouriana* is overwhelmingly dominant, with *P. monticola* as a consistent associate. A typical stand is at Sunrise Pass (2100-2300 m). The understory includes scattered clumps of *Arctostaphylos nevadensis* and *Quercus vacciniifolia.* Common herbs are *Astragalus whitneyi* ssp. *siskiyouensis, Castilleja aracnoides* and *applegatei, Orthocarpus copelandii, Lomatium macrocarpum, Epilobium obcordatum* ssp. *siskiyouense, Aster ledophyllus, Sitanion hystrix, Oxyria digyna, Linum lewisii, Crepis pleurocarpa, Lupinus croceus, Phlox diffusa,* and *Arenaria nuttallii* ssp. *gregaria.* The overall aspect of the high Red (ultrabasic) Trinities is very different from that of the White (granite) Trinities: the widely-spaced trees, often gnarled and bizarrely shaped, and the floristically rich though sparsely vegetated understory produce a profound visual impression.

Packer's Peak, the only metamorphic mountain reaching the subalpine zone, is also vegetationally unique in harboring *P. balfouriana, P. albicaulis,* and *T. mertensiana* all in one place. There also a very rich shrub flora, including *Cercocarpus ledifolius, Holodiscus microphyllus, Ceanothus velutinus, Chrysothamnus nauseosus, Haplopappus bloomeri,* and *Purshia tridentata.* The herbaceous flora is also diverse, containing elements of both the granitic and ultrabasic floras, including the extremely rare endemic *Penstemon tracyi.*

Space prohibits further discussion of the structure of Trinity Alps vegetation. Because few of the butterflies are very narrowly restricted altitudinally and because so large a proportion of the fauna is associated with non-forested habitats, we have adopted only a very loose "zonal" system of reference which recognizes foothill (including riparian canyon), montane coniferous forest (Ferlatte's "Mixed" plus "Red Fir"), subalpine, and alpine. See "Zonal Relationships," below.

Mount Eddy

Mount Eddy (2738 or 2750 m, two figures recently quoted) is the highest ultrabasic peak in northern California and has been mapped in both the Klamath and Cascade Provinces. It is part of the ultrabasic Trinity Pluton which includes much of the Trinity Divide. The summit (122°27'W, 41°20'N) is 27.4 km WSW of Mount Shasta and 59.6 km ENE of Thompson Peak. It is separated from the Trinity Alps by the lower, but still rugged, Trinity Divide which penetrates the subalpine zone barely at Gumboot Butte (2048 m).

Being farther east than the Trinities, Mount Eddy receives less rainfall. This is reflected in the conspicuous dominance of *Artemisia tridentata* from Deadfall Meadow up to tree line. This plant, which is completely absent from the Trinities, forms an understory in Red Fir forest, pure stands on sandy benches and arid slopes at Deadfall Lakes, and a distinctive association with *Cercocarpus ledifolius* in the subalpine zone, most conspicuously on the south slope of the south arm of Mount Eddy. The uppermost subalpine forest is almost identical in aspect to that of the Red Trinities, composed of *Pinus balfouriana* and *P. albicaulis*. It is very open and its understory grades insensibly into alpine fell-field, which is undisputably present on Mount Eddy. Above tree line the vegetation includes *Astragalus whitneyi* ssp. *siskiyouensis, Epilobium obcordatum* ssp. *siskiyouense, Eriogonum alpinum, Campanula scabrella, Hulsea nana, Cirsium drummondii, Crepis pleurocarpa,* and *Draba aureola.* At the very summit there are large prostrate mats of *Potentilla fruticosa* in a unique alpine habit.

A flora of Mount Eddy is available (Whipple and Cope, 1978), prepared as a tool for defining a Research Natural Area; 11 of 48 proposed "sensitive" (rare, endangered, or endemic) plant species in the Shasta - Trinity National Forest occur there.

From Deadfall Meadows to about 2350 m occur a series of boggy meadows of the ultrabasic type, vegetationally similar to those in the Red Trinities. They share the rare endemic Composite *Railardella pringlei.* Some of the hillside-seep bogs on Mount Eddy are larger than any in the Trinities and are especially striking because they occur adjacent to almost pure sagebrush.

Scott Valley

Scott Valley lies in the rain shadows of the Trinities, Mount Eddy, and Mount Shasta, which allow for a major southwestward penetration of Great Basin vegetation into California. The floor of the valley is mostly agriculturalized, with a few relict sedge marshes. The natural vegetation is described by Vasek and Thorne (1977). Because exposure and the airstreams around the mountains play so critical a role here, bizarre mixtures and juxtapositions of vegetation types are common. The dominant shrubs are *Juniperus occidentalis, Purshia tridentata,* and *Chrysothamnus nauseosus. Artemisia* is mostly lacking, although it is common north of Mount Shasta. On moister sites juniper mixes with and intergrades to *Pinus ponderosa - P. jeffreyi - Quercus garryana* forest; the same sequence is repeated on the approach to Mount Eddy from the north, on Stewart Springs Road. *Ceanothus cuneatus* occurs as an understory and successional plant with this forest. North from the Edgewood -

Gazelle area there is an extensive treeless grassland. Apart from low precipitation, winters north of the mountains are much colder than at comparable elevations to the south.

Phytogeography of the Trinity - Eddy Region

Stebbins and Major (1965) divided California into ten biotic provinces and examined the distribution of relict plant taxa among them. They found two major centers - the Klamath Mountains and the north and west borders of the Colorado Desert - which each accounted for 26-30% of all the relicts in the state. The high degree of relictualism and endemism in the Klamath Mountains has been known for many years. The predominant group of relicts is of Arcto-Tertiary derivation (Axelrod in Munz, 1970). Whittaker (1960) pointed out that relictualism and endemism in the Siskiyou Mountains were related to climate and soils. The two are best considered together. "Serpentine (ultrabasic) endemism" has generated a very large literature (Proctor and Woodell, 1975, present a 16-page bibliography) and only a very brief sketch of the origins and role of the phenomenon in the Trinity - Eddy flora is possible here. Ultrabasic endemics fall into two groups: those which evolved *in situ* on ultrabasics and those whose present distribution is relictual from a previously wider distribution on non-ultrabasics. Kruckeberg (1969) accounts plausibly for the evolution of plants of the former type by a sequence of adaptation to serpentine, depletion of "biotypes," and differentiation of local populations. This is a suitable model for herbaceous genera like *Streptanthus* (Cruciferae). It need not apply to woody taxa like Sargent Cyrpess (*Cupressus sargentii*) or Serpentine Scrub Oak (*Quercus durata*), which have a paleobotanical record clearly establishing a former widespread range on non-ultrabasics. Understanding the present restriction of these plants to serpentines may require integration of Pleistocene climatic change into the picture. Axelrod (1977, p. 152) reviews several taxa, showing what he interprets as a process of retreat into low-competition (ultrabasic) habitats as climatic change tilts the competitive balance away from formerlysuccessful species.

Axelrod (1977, pp. 154-157) also interprets the high montane and subalpine relict trees of the Klamath Province in Quaternary terms: "Their presence appears to reflect the gradual shift southward to a shorter precipitation season, less summer rain, and greater ranges of temperature which increase drought stress." It seems plain that the frequency of cloud cover and summer rain has been a controlling factor in Quaternary and Recent plant distributions in California. One of the most intriguing relicts in the state is Foxtail Pine, *Pinus balfouriana*, a characteristic subalpine tree on ultrabasics in the Trinity - Eddy region (it occurs on Lake Mountain, Russian Peak, Scott Mountain, Mount Eddy, Eagle Peak, Red Rock Mountain and Sunrise Pass, Packer's Peak, Gibson Peak, and North Yolla Bolly, 2000-2750 m) which occurs disjunctly in the southern Sierra Nevada at 2600-3660 m on shallow decomposed granite soils in Tulare and Inyo Counties (Mastrogiuseppe, 1972). Axelrod notes that some herbaceous associates show related distributions, sometimes as species pairs. He concludes that the presence of *P. balfouriana* and similar species "in the southern high Sierra Nevada seems related to the fact that there is considerably more warm season precipitation there than in the central Sierra. Farther north the Sierran axis is so low that subalpine environments are highly restricted. Sites there were strongly affected by the Xerothermic, which may have eliminated possible intermediate links between the Klamath and southern High Sierra regions."

Despite the concentration of endemics in the Klamath Province, the actual numbers of species involved are low. Thus, of 571 vascular plants recorded in the Trinity Alps by Ferlatte, only 7 were strictly endemic to the Klamath Province; 4 of these also occur on Mount Eddy (Whipple and Cope, 1978). Phytogeographic analysis in Ferlatte's book is restricted to one paragraph on p. 9, which is worth quoting in its entirety: "The flora of the Trinity Alps is generally typical of the high mountains of California: 77% of the species collected occur in the Sierra Nevada; and 84% extend at least to Oregon with many species reaching as far north as Alaska. There is some influence from the east with 17% occurring in northeastern California and 13% ranging as far as the Rocky Mountains; 12% reach the southern limits of their ranges in northwestern California without occurring in the Sierra Nevada; and 8% of the species collected are restricted to California. The presence of species like *Arnica viscosa, Claytonia nevadensis, Haplopappus lyallii, Picea breweriana,* and *Pinus balfouriana* suggests that some elements of the flora may represent relicts of older populations that existed in past, cooler climates."

The past changes in distributions of organisms are complex, and the interpretation of relicts not necessarily straightforward. Some are easier than others. *Hulsea nana* is restricted in California to Mounts Lassen, Eddy, Shasta and Goosenest. It is widespread in the Cascades (Hitchcock and Cronquist, 1973), north to Mount Rainier, and in the Wallowa Mountains (Munz, 1970). *Campanula scabrella* is known in California only above tree line on Mount Eddy, but occurs in the Oregon and Washington Cascades and east to Idaho and Montana (Hitchcock and Cronquist, 1973). *Astragalus whitneyi* is isolated on serpentine on Mount Tedoc, Tehama County, where there is also a strict endemic *Haplopappus* (*ophitidis*) very closely allied to *H. bloomeri.* Other species occur disjunctly in the Trinity bogs and bog meadows and in the very isolated bogs and bog meadows of the Yolla Bollys and North Coast Range, including Plaskett Meadows (Hemphill, 1952, 1971). All of these relicts can be interpreted in terms of northward retreat of a flora basically incapable of dealing with lack of summer rain, a process Axelrod and Daubenmire (1977) find important in the evolution of the Californian and Pacific Northwest floras, respectively. Inferring directionality from Klamath - Sierran disjunctions is much more difficult. Ferlatte found several species in the Trinities hitherto reported in California only in the Sierra Nevada. If we consider the alpine and subalpine taxa, *Arnica mollis, A. amplexicaulis, A. diversifolia, Artemisia norvegica* var. *saxatilis, Lupinus lyallii,* and *Carex scopulorum* all occur in the Cascades, usually far northward; *Carex proposita* has a spotty distribution in central Idaho and the Wenatchee Mountains, Washington; and *Saxifraga bryophora* is unrecorded outside California. To what extent can we infer from the presence of these species in the Trinities that they colonized the Sierra from the north? Howell (1944) found similar disjunctions between the Marble Mountains and the Sierra, and Clark (1972) gives additional ones from the Siskiyous. We will return to the origins of the high-altitude Sierran flora and its relationships with the Trinity - Eddy area in the discussion of butterfly biogeography, below.

Miller (1951) analyzed the avifauna of the Californian biotic provinces and found the largest "boreomontane" component in the Klamath region. His overall analysis mirrors Ferlatte's for the sources of the Trinity flora. Given the assumption of higher dispersability in birds than in most plants, the similarity suggests current rather than past ecological regimes as the greater control on the distributions of both.

Butterflies are intermediate between plants and birds in dispersability; like birds they are often interested in the structure of vegetation, but unlike birds they commonly are tied to one or a few specific plant species. Comparisons among the three groups should, then, be instructive.

The Problem of the Sierran Alpine Biota

How does an alpine biota originate? Speaking of alpine floras, Chabot and Billings (1972) said: "The Sierra Nevada of California is one of the few situations where such a question may reasonably be studied. In this young mountain range the areas of alpine habitats are extensive, and the well-developed alpine flora is uniquely composed of a large endemic and locally derived element and a relatively small cosmopolitan arctic-alpine group (Major and Bamberg, 1967). A floristic array so truly alpine and with such a small arctic component does not occur in any other North American mountain system."

Do these characteristics pertain to the Sierran alpine butterfly fauna? For Yosemite National Park, Garth and Tilden (1963) list 51 species as resident in either the "Arctic-Alpine" or "Hudsonian" (alpine and subalpine) life zones. Where does this fauna come from? There are three plausible sources which could contribute to it: evolution *in situ* from pre-existing regional lowland sources; invasion from the north during the Pleistocene; and invasion from the Rocky Mountains across the Great Basin. The third of these is least familiar to entomologists, though it has generated a lively controversy among phytogeographers. It emerged with the publication (Major and Bamberg, 1963, 1967) of the Convict Creek flora. In this subalpine limestone drainage on the Sierran east slope in Mono County occur *Arctostaphylos uva - ursi* at its only station in the range, *Draba nivalis* var. *elongata, Kobresia myosuroides, Salix brachycarpa,* and *Scirpus rollandii,* the last four not known elsewhere in California, but disjunct from the Rockies, the eastern Great Basin, and the Wallowas - North Cascades. *Pedicularis crenulata* occurs at its only California station near the mouth of Convict Creek, disjunct from the Rockies. Major and Bamberg proposed that this extraordinary constellation of relicts marked a Pleistocene dispersal track from the Rockies to the Sierra via the Great Basin, perhaps in boggy swales similar to modern subalpine meadows; they envisioned a Great Basin cold steppe similar to modern climates in central Asia. This would allow for direct biotic enrichment of the high southern Sierra without postulating that elements shared with the geologically much older Rocky Mountains were derived by migration from the north.

Major and Bamberg's hypothesis has not been enthusiastically received. Chabot and Billings (1972) felt that the entire Convict Creek assemblage came from the north and persisted on the unusual soils of that basin because of a lack of competition from the dominant flora of the granodiorite of the remainder of the range. Raven and Axelrod (1978, p. 63) concur: "There is so little similarity between the flora of the Sierra Nevada at large and that of either the northern or southern mountains of the Great Basin that such a path of migration appears highly unlikely. The decreasing proportion of Rocky Mountain species southward in the Sierra Nevada, coupled with the increasing proportion of endemism (Stebbins and Major, 1965), accords much better with a pattern of migration from the north." Earlier, Axelrod (1976, p. 34-37) discussed the matter in great detail and concluded that paleontological evidence does not support the postulated cold-steppe climate required by Major and Bamberg, and that acceptance of their hypothesis would create far greater problems than it solved. However, Major and Taylor (1977) review the alpine floras of California and conclude that the Great Basin dispersal route must be considered still a possibility.

Quantitative similarities among various Far Western alpine floras, from Alaska to southern California, are presented by Major and Taylor in the form of a plexus diagram (1977, fig. 18-1, p. 612) combining data from a variety of sources. Using Sorensen's (1948) coefficient of similarity, a derivative of Jaccard's (1902) coefficient of community, they show that "three major floristic units are apparent: a North Cascade, a South Cascade, and a Sierra Nevadan unit. Of the California localities, the alpine flora of the high peaks of the Klamath Mountains is more similar to that of the Northern Cascades than to that of either of the Southern Cascade volcanoes, Mount Shasta and Mount Lassen, or to the Sierra Nevada. Several important Pacific-Cordilleran species, like *Saxifraga caespitosa* and *Haplopappus lyallii*, are known to occur in California only in the Marble Mountains and Trinity Alps. Mount Shasta and Mount Lassen are most similar floristically to the other inland southern Cascade volcanoes, Mount Mazama (Crater Lake) and the Three Sisters. The Sierran alpine flora is a distinctive unit, largely because of the high proportion of endemic species....Chabot and Billings attribute the present composition of the alpine flora of the Sierra to six predominant variables (1972, p. 174):(1) recent uplift of the range, (2) isolation of the range from preexisting sources of alpine species, (3) restriction of species migrations by Pleistocene glaciations and (4) by post-Pleistocene climatic shifts, (5) mixing and telescoping of alpine and desert floras during Pleistocene migrations, and (6) the present summer aridity of the Sierran alpine climate." They also reproduce (table 18-2, p. 610) a breakdown of the phytogeographic affinities of the Sierran alpine flora, showing 3.8% of the species as truly "boreal," 14.2% Arctic-Alpine, and 82% "Alpine," decomposing into 64% cordilleran (7.3% Beringian, 17.3% Rocky Mountain species) and 17.9% "western," of which 7.3% are "widespread western" and 10.6% Great Basin. Nearly a sixth of the flora is endemic, and another sixth occurs in the Sierran-Cascade axis only.

The distinctness of the Sierran alpine flora is thus amply documented, but its derivation remains controversial despite an abundance of speculation.

The Sierran Alpine Butterfly Fauna

Now we may return to the Sierran alpine butterfly fauna and examine its characteristics. Only three species are "good" Sierran endemics: *Oeneis ivallda, Colias behrii,* and *Hesperia miriamae* (also in the White Mountains). All of these belong to circumboreal genera, and their interpretations all present serious biosystematic problems. *Hesperia miriamae* seems most closely related to *H. nevada* (MacNeill, 1964), which is disjunctly distributed in the Rockies, the high Sierra,the Charleston Mountains of southern Nevada, the Warner Mountains, various parts of the Oregon and Washington Cascades and the Wallowas, Vancouver Island and southern British Columbia. The populations east and west of the Great Basin are phenotypically differentiated. Here, then, we appear to have a locally derived endemic from a northern source. *Oe. ivallda* is closely allied to *Oe. chryxus,* the most widely distributed member of the genus in North America. Its precise relationship with what has been called *Oe. c. stanislaus* remains uncertain. Hovanitz (1940) and Garth and Tilden (1963) regarded them as conspecific, while Emmel (in Howe, 1975) did not. The range of *stanislaus* (Carson Pass to Echo Pass) is completely contained within that of *ivallda*, which reaches north to Donner Pass. We will sidestep this problem by lumping them under *ivallda*; if they are distinct this would cause us to underestimate the degree of Sierran endemism. *Colias behrii* is a member of the *Vaccinium*-feeding complex and is a derivative of *C. palaeno, pelidne,* or *interior*. The nearest extant populations of these are: *palaeno*: northern British Columbia; *pelidne*: eastern B.C., Montana, Idaho, and NE and WC Wyoming; *interior*: Canadian Zone in Washington and Oregon. Despite the contiguity of *interior*, our impression is that *behrii* is closest to *palaeno*. This problem can be addressed by a phylogenetic analysis of the group, including the early stages, wing pigments, and any other useful data.

At the subspecies level, the Sierran alpine fauna contains the obvious circumboreal relict *Lycaena phlaeas hypophlaeas*, disjunct from the High Sierra to the Wallowas in northeastern Oregon; *Chlosyne damoetas malcolmi* of the central and southern Sierra, only weakly distinguished from nominate *damoetas* in Wyoming, Colorado, B. C. and northeastern Utah; and several subspecies of *Euphydryas editha* and *chalcedona* whose affinities are obscure within these immensely complicated groups. *Plebeius shasta* is moderately differentiated in the High Sierra (*comstocki*) but occurs in typical form in eastern Oregon, Washington, and Idaho and in Nevada.

Lycaena editha and *L. cupreus* are subalpine or alpine species at the latitude of Yosemite (Garth and Tilden, 1963) but both are montane at Donner Pass and northward (Emmel and Emmel, 1962; Shapiro, unpublished). Both extend to the north and northeast of California. *L. cupreus* has to have come from the north, since the Rocky Mountain populations at this latitude are the quite distinct subspecies *snowi*, a high-alpine resident that far south but descending to moderate elevations in Wyoming. Its range as a species reaches southeastern Alaska and there are closely related species in central Asia. *L. editha* belongs to a strictly Nearctic group of considerable antiquity, as shown by the disjunction between the ranges of *L. xanthoides* on the Pacific slope and *L. dione* in the midwest. The present distribution of *editha* supports a northern route. *Agriades "glandon"* or *"aquilo"* belongs to another circumboreal complex whose taxonomy is, as usual, muddled. The Sierran entity, *podarce*, has been interpreted as extending north into Oregon while the more boreal entity *megalo* extends south into Washington. The distinct subspecies *rustica* is in the central and southern Rockies, south to New Mexico; it differs from the more westerly ones in habitat as well as facies. F. Michel (*pers. comm.*) claims to have found *rustica* and *podarce* parapatric in different habitats in Utah, suggesting that our assemblage includes at least two species. Again, phylogenetic analysis is needed, but there is no reason to doubt a northern dispersal route for this complex into California.

In summary, the Sierran alpine fauna includes: one circumboreal relict (*L. phlaeas*) clearly derived from the north; an endemic (*C. behrii*) whose most probable ancestor (*C. palaeno*) is far to the north; several species whose distributions are not inconsistent with dispersal from either the north *or* the east, but are less conjectural with a northern route (*Oe. ivallda, P. shasta, L. cupreus, L. editha, A. glandon, C. damoetas*); one endemic (*H. miriamae*) apparently derived from a species (*H. nevada*) which colonized the Sierra from the north; and several obscure *Euphydryas*. Some additional components of the high-altitude Sierran fauna are discussed in the next section.

The interpretation of this fauna could potentially be modified by discoveries in the Trinity - Eddy Region. We have already seen that plant relicts and disjunctions between this area and the High Sierra are not uncommon. Axelrod (1976) says: "Spreading montane Mediterranean climate not only restricted many taxa in the Sierra during the later Quaternary, and eliminated others, but it probably accounts for the present restricted range of the Rocky Mountain - Cascade conifers in the Klamath - Siskiyou region. As compared with the Klamath - Siskiyou region, the lower forest diversity in the Sierra, which results chiefly from the higher summer evaporation rate there, seems attributable to spreading montane Mediterranean climate. So far as woody plants are concerned, the Klamath - Siskiyou region is basically a reservoir into which have poured taxa from diverse sources, which have persisted there in favorable sites under a climate more like that of the late Quaternary than elsewhere in the Far West." It would thus not be unreasonable to expect important butterfly relicts there, too.

Comparisons Among Faunas

Let us first consider the overall faunal similarities. In table 1 the combined faunas of the Trinity Alps and Mount Eddy are compared with comprehensive faunas, both published and unpublished, for one area to the north (Crater Lake National Park, Oregon) and several to the south. These comparisons must be qualified. First, a subjective decision was made as to the distinctness of subspecies, and those which we judged to be clinal or ambiguous were not listed separately. This has the potential to cause an underestimate of endemism, or an overestimate of similarity. Second, the areas represented by these faunas differ, but species - area relationships cannot be precisely determined. Within each area sampling was done only in selected sites - selected for habitat types, "representativeness," and accessibility - and only subjective estimates of the adequacy of coverage of the larger area can be made. Nonetheless, granted the much larger area of the Sierra Nevada, the Trinity - Eddy fauna (116 species and subspecies) is clearly rich; Yosemite National Park, covering the entire set of altitudinal zones on both slopes of the Sierra, has 148 and the South Yuba River country, covering the same set of zones as the Trinities but including Donner Pass (102, for its size one of the richest faunas in temperate North America), has 124. Table 2 shows the similarities among the faunas using three commonly used, simple indices of faunal resemblance - Jaccard's (1902) coefficient of community, Simpson's (1943) index, and Sorensen's (1948), both more useful if the sizes of the faunas differ markedly. Using all three, the Trinity - Eddy fauna is more similar to Crater Lake than to any of the Sierran ones. At the subspecies level, 71 of 80 entities at Crater Lake also occur in the Trinity-Eddy fauna; at the species level the resemblance is even greater. In the Sierra the closest affinities are to the Lang Crossing (mid-elevation) and Yuba Pass faunas, both in the north. This reflects not only geographical proximity but the preponderance of montane taxa in the Trinity-Eddy fauna, and the relatively low level of endemism in the montane fauna. We proceed to consider only the subalpine and alpine faunas in tables 3 and 4; here the level of differentiation is higher.

We have separated the Trinity and Eddy high-elevation faunas and compared them to each other and to the subalpine-alpine faunas of Donner Pass + Castle Peak and Yosemite. As expected, the Trinities and Mount Eddy resemble each other much more strongly than either resembles the Sierra, but Mount Eddy resembles Donner + Castle more strongly on all indices than any other between-region comparison. This probably reflects continentality of climate rather than a historical connection - there are no relicts to suggest that Mount Eddy was a stepping-stone between the ranges, and only the intermediate population of *Satyrium fuliginosum* to suggest genetic connections across it.

We found no "Sierran" endemics in the Trinity - Eddy region at all. All of the High Sierran endemics - *Oe. ivallda, C. d. malcolmi, C. behrii, H. miriamae* - are absent; so is *L. phlaeas*, which jumps to the Wallowas; so is *Plebeius shasta*, which goes up the east side of the Sierra north of Castle Peak through Plumas and Lassen Counties, and occurs in the Warners; and so, strikingly, are *L. cupreus* and *L. editha*. The northern range of *cupreus* is poorly understood north of Plumas County, but *editha* occurs in southern Siskiyou County (Bartle - McCloud - Hambone area); both it and *cupreus* extend northwestward to Crater Lake (Tilden and Huntzinger, 1977). *L. editha* actually occurs as close to our study area as Dunsmuir, Castle Lake, and Mount Shasta City.

Several species occur in the Trinity-Eddy and Sierran high country, but the subspecies are different: *Speyeria egleis, S. mormonia, Euphydryas editha, Satyrium fuliginosum, Parnassius phoebus, Thorybes mexicana, Hesperia harpalus,* and *Polites sabuleti*. The most spectacular of these is *S. mormonia*. We were amazed to find *S. m. erinna*, the eastern Cascade - Wallowa subspecies of Oregon, at Deadfall Lakes - a range extension of 120 km. Sierran *S. m. arge* reaches its northward limit near Yuba Pass. The Trinity-Eddy subspecies of all the complexes listed above extend north into Oregon, except perhaps *S. fuliginosum* (whose range may be coterminous with that of its endemic host, *Lupinus croceus*). *Polites sabuleti* is especially intriguing because it occurs as an isolated relict population at Plaskett Meadows, Glenn County, along with *Parnassius clodius*, 120 km SSW of its Trinity range. This is an extremely isolated boggy meadow; the occurrence of disjunct species there implies northward retreat from a formerly more extensive range (Hemphill, 1971). *Agriades glandon* is sufficiently different in the Trinity-Eddy region to be nameable as a weak subspecies distinct from *podarce*. The females of *Lycaena heteronea* are exceptionally variable, the underside markings tend toward ssp. *gravenotata*, and the Trinity-Eddy phenotypes extend to the Yolla Bollys (S.O. Mattoon, *pers. comm.*) and to the isolated relict populations in the Coast Range south to Marin County. Two very widespread high-altitude species, *Callophrys lemberti* and *Pieris occidentalis*, show subtle differences between the Trinity-Eddy and Sierran phenotypes, the latter as part of a long cline starting in arctic Alaska.

At least three montane species (*Lycaena arota, Habrodais grunus,* and *Cercyonis silvestris*) appear to have clines across the study area, associated with the moisture gradient. We have no basis to discriminate between primary and secondary intergradation in these cases. All the species are somewhat colonial. At higher elevations three species - *S. fuliginosum, S. egleis,* and *T. mexicana* - also seem to be clinal. *Fuliginosum* has already been mentioned. *S. egleis oweni* is most distinct to the east, on Mount Eddy and Mount Shasta, while Trinity specimens tend to look more like *S. e. egleis* of the Sierra. At present we cannot discriminate between parallelism and a historical connection providing a source of *egleis* genes. In *T. mexicana*, Mount Eddy specimens are more typical *aemilia* than Trinity ones - which depart even further from the Sierran *nevada* phenotype.

No one seems to doubt that *Pinus balfouriana* entered the Sierra from the north. It is a very long-lived tree - over a millennium - but the Sierran and Klamath populations are phenotypically and physiologically different (Mastrogiuseppe, 1972 and D. Axelrod, *pers. comm.*). The degree of differentiation observed between Trinity-Eddy and Sierran conspecifics should not be surprising given the much more rapid turnover of butterfly generations. However, this differentiation is equally compatible with northern and eastern origins for the Sierran fauna. How significant, then, are the absences of Sierran endemics from the Trinity-Eddy area as an argument for double colonization of California?

Types of Absences

There are two sets of hypotheses to account for the absence of a species from a given area:

1. It never occupied the area at all. (It was unable to reach it due to physiographic or climatic barriers, or sheer distance; or it had access to it but was excluded by either abiotic or biotic factors, such as climate and competitors.)
2. It was formerly present but became extinct. (Either abiotic or biotic factors could be responsible; or if the area occupied was small, extinction could occur purely by chance.)

Were the Trinities too remote from potential source regions to be colonized by the Sierran fauna? If colonization was from the north this seems very unlikely, since to reach the Sierra the species would have had to pass down the Cascades immediately to the east. The relatively low country and the long distances between the Trinity-Eddy area and Yuba Pass could, however, easily have hindered or prevented *northward* colonization by a fauna invading via the Great Basin, as suggested by Major and Bamberg. There are no potential competitors to exclude the Sierran endemics were they to be introduced today.

The extent of subalpine and alpine habitat in the Trinities is small, but it must have been greater when climatic snowline was depressed some 300 m. If the alpines were there at that time they would have retreated upslope and perhaps become extinct as suitable habitats became limitingly small. However, it is striking that so large a segment of the Sierran alpine fauna persists at its northern limit, on the small, isolated alpine area of Castle Peak (Shapiro, 1977). The extinctions, if extinctions there were, would probably have involved the climatic differences between the Klamath and Sierran alpine zones.

What limits those "Sierran" species which have access to the Trinity-Eddy area today, but fail to colonize it? *Lycaena editha* gets within 12 km of Mount Eddy. Emmel and Emmel saw it oviposit at the widespread weed *Rumex acetosella* at Donner Pass in 1971. This plant is common in the Trinity-Eddy area. It is, however, a fairly recent introduction in the California flora, and *L. editha* must have had a pre-European host. In the Sierra we have found it using *Polygonum phytolaccaefolium*, a common montane - subalpine species which ranges north to subarctic Alaska; it occurs at both Mount Shasta City and Bartle but has never been found in the Trinities or on Mount Eddy, even though it goes around them to the north into the Siskiyous (Major and Taylor, 1977, p. 621-23; Sawyer and Thornburgh, 1977, p. 708). It *could* be a limiting factor on the westward spread of *L. editha* in the Trinities, but this merely pushes the question back one level - why is *P. phytolaccaefolium* absent? The weed *R. acetosella* is also a host plant of *L. cupreus*, which has a similar distribution but has not been noted as associated with *P. phytolaccaefolium*. Chabot and Billings (1972) investigated the Sierran alpine flora from a physiological standpoint, and physiological adaptation to climate is probably just as important in butterflies, though more difficult to study. It is plain, for example, that the large populations of *Colias philodice eriphyle* and *Lycaeides melissa* in Scott Valley have access to the Central Valley of California, with its extensive alfalfa plantations, through the lowlands along Highway 3; but they make only very feeble penetrations beyond Callahan, presumably for physiological reasons.

The same climatic characteristics which make the Klamath Province a reservoir for relict plants could be inimical to the butterfly fauna: increased cloudiness and precpitation, including that during the growing season. The butterfly faunas of the rainy western slopes of the Pacific Northwest, from northern California to the Alaska Panhandle, are notoriously depauperate despite high floristic diversity and endemism. Even if present climates were not limiting, the Pleistocene Klamath Province could have been intolerably wet and cloudy for butterflies, so that the invaders from the north passed along the Cascade - Sierran axis and failed to enter the Trinities at all. (The Trinity fauna includes several Arcto-Tertiary species at montane levels - *Pieris napi, Habrodais grunus, Celastrina argiolus* - which may have reinvaded from the Coast Range after being driven out by severe Pleistocene climate. This is consistent with the variation of *H. grunus* and especially with the geography of *P. napi* subspecies in the region; Shapiro, unpublished).

A number of prominent circumboreal butterfly groups or species of the central Rockies are totally absent from California (indeed, on the Pacific slope south of Washington): *Pyrgus centaureae,* several *Colias* and *Oeneis*, the genus *Erebia*, and *Euphydryas gillettii.* At present it is impossible to determine whether any of these could plausibly have entered California and become extinct: the general east-to-west diminution in the boreal butterfly fauna of the west has the same two sets of explanations as the absence of the Sierran endemics from the Trinity-Eddy region.

The Trinity-Eddy and Sierran butterfly faunas are more differentiated from each other than the avifaunas. From Miller's (1951) table 7 we find 49 bird species in common, out of totals of 57 (Trinity) and 72 (Sierra). These give Jaccard and Simpson coefficients of 61.25% and 85.97% respectively (the highest Trinity-Sierra values are with Lang Crossing, 55.88% and 79.17%). Most of the difference in the avifaunas is due to the "non-boreal" components (10/57 Trinity vs. 18/72 Sierra); only two shared species are "non-boreal."

Butterfly Biogeography: Conclusions

The Quaternary biogeography of the Far West is in far from a satisfactory state, even though more complete scenarios of past floristic changes exist there than elsewhere in the Nearctic. Frustrated butterfly biogeographers may note the ongoing controversies among paleobotanists, who have extensive fossil and subfossil evidence, and be heartened that in the absence of fossil evidence they are able to develop scenarios at all. It is now plain that the relictualism of the Klamath flora is not matched in the butterflies, and we must integrate this fact with the floristic scenarios in an acceptable way.

The proportion of "Rocky Mountain" butterfly taxa *increases*, not *decreases*, southward in the Sierra Nevada. The Sierran high-altitude fauna is mostly not derived from regional lowland sources, unlike the flora; it is the result of long-range dispersal and subsequent differentiation. There are two "Rocky Mountain" relicts in the north state to challenge our set of generalizations - *Polites themistocles* and

Euphyes vestris - but both are in the Bartle area of Siskiyou County, not in the Klamath Province, and both are montane, not subalpine or alpine. (This area is also notable for the relict occurrence of the northern Dolly Varden Trout, *Salvelinus malma.*) In California *vestris* is a very remarkable relict, occurring in the coastal fog belt in Santa Cruz, Sonoma and Mendocino Counties, and again in seep habitats in San Diego County and Baja California Norte; Emmel and Emmel (1973) state that the northern and southern populations are phenotypically different. *P. themistocles* seems to be known from only the one station at this time. Neither seems to be of any use in interpreting Trinity-Sierran patterns.

Forthcoming books on the butterflies of the Rocky Mountain region and the Pacific Northwest will provide vital data to assess the distributions of California taxa in a regional context. Based on what is availabe *now*, we are forced to the following conclusions:

1. The high altitude (subalpine and alpine) butterfly faunas of the Trinity - Eddy region and the Sierra Nevada are strongly differentiated - definitely more so than the respective avifaunas and perhaps more so than the floras.

2. Where a species is differentiated into subspecies in the Klamath and Sierran faunas, the former extends into Oregon while the latter is a Sierran endemic, mostly occurring in the high country south of Yuba Pass.

3. The butterflies are not dependent on plant taxa for which paleobotanical data are available, and with a very few exceptions are not associated with plants whose distributions are relictual or endemic.

4. There are no distributional phenomena in the butterflies which are absolutely incompatible with Major and Bamberg's hypothesis. The bulk of *positive* evidence (living relicts) favors a generalized northern route into the Sierra, with subsequent (Xerothermal?) extinctions of many taxa in the lower northern part. The *negative* evidence (complete absence of alpine or subalpine relicts in the Trinity - Eddy fauna) is more consistent with the eastern route, but there are several potential explanations available.

5. In view of the broader problems posed by Major and Bamberg's hypothesis we tend, somewhat reluctantly and provisionally, to agree with Axelrod (1976, 1977) and Raven and Axelrod (1978) that the northern route is more likely. We are unable to determine if the absence of "Sierran" butterflies in the Klamath Province is primary or secondary.

We note, finally, that no one has yet examined the trans-Beringian butterfly faunal connections in a systematic manner. Several groups with largely subalpine or alpine distributions in western North America (*Pieris occidentalis*, Shapiro, 1980; *Lycaena cupreus; Neominois ridingsii*) show clear affinities with Central Asian taxa and indications of past circumboreal distribution in cold steppe or periglacial steppe-tundra like that envisioned for the Great Basin by Major and Bamberg. These connections should become more apparent as the Central Asian fauna and literature become better known to American workers and as the Alaska Lepidoptera Survey continues to document the extent of present trans-Beringian interchange.

Zonal Relationships and Altitudinal Anomalies

The Nearctic butterfly literature has been strongly influenced by Merriam's (1898) "life zone" concept, which pervades much of western natural history. It was applied consistently by Garth and Tilden (1963) in their treatment of Yosemite butterflies, although they were obliged to express the west-east slope dichotomy in terms of Dice's (1943) biotic provinces, and Merriam's zones tend to break down on the Great Basin side. Even in Yosemite, Garth and Tilden were obliged to acknowledge (p. 77) the existence of "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 consideration." There has been a general movement in American plant ecology for some 25 years away from classificatory schemes and toward an "individualistic" approach to species distributions (see Gleason, 1939): a benchmark paper in this direction was Whittaker's analysis of Siskiyou Mountains vegetation (Whittaker, 1960). Life zones are a useful pedagogic device, but their correspondence to coevolved, repeating ecological units is questionable. Paleobotanical evidence (Axelrod, 1977; Raven and Axelrod, 1978) is unequivocal in showing that communities or associations have formed, fragmented, and reformed in novel combinations throughout the geologically and climatologically unstable Quaternary. The present life zones can be seen in this context as merely transient assemblages of species whose physiology and distributional history permit them to co-occur in the climates that exist at the moment.

Although there are broad similarities between Sierran and Trinity-Eddy vegetation, translation of Garth and Tilden's life-zone analysis of the Yosemite butterflies to the Trinity fauna is almost impossible. The problems are the same as described vividly by Hemphill (1971) for the Yolla Bolly vegetation: "The Yolla Bolly Range is so abrupt and narrow that zonal conditions are telescoped together. To the east lie the heated foothills, and on the west the mountainside is swept by cool winds....In the vicinity of Black Butte, Upper Sonoran and Canadian conditions lie within three miles of one another. This tends to produce a greater mixture of floral and faunal elements than one finds in the broad, gradual slopes of the Sierras....Any attempt to separate the Transition and Canadian elements in the life of this region does violence to the natural grouping, as most species occur throughout the extent of the coniferous forest belt....a large number of associations are involved in a complex mixture of bewildering confusion....The mixed forest area offers one of the most difficult problems to the ecologist who tries to interpret field conditions in terms of Merriam's life zones....the mapping of the life zone distribution cannot but be inaccurate."

A number of butterflies occur at higher elevations in the Trinity - Eddy region than they or their close relatives do in the Sierra, despite the fact that the range is farther north and that many plant communities extend lower. These include *Cercyonis silvestris* (to 2100 m), *C. pegala boopis* (1545 m), *Coenonympha tullia eryngii* (2200 m), *Habrodais grunus* (2000 m), *Satyrium californica* (2275 m), *Pieris napi* (2100 m), *Hesperia columbia* (1600 m), *Thorybes pylades* (1430 m), and *Epargyreus clarus* (1400 m). (Weedy species like *Plebeius acmon* and *Colias eurytheme* occur more consistently at high elevations in the Trinities because of the short dispersal distance from the lowlands, but they do not overwinter.) Other species follow their plant communities to lower elevations than in the Sierra: *Chlosyne hoffmanni* (to 1400 m), *Agriades glandon* (1500 m), *Pieris occidentalis* (850 m in Scott Valley), *Parnassius phoebus* (2040 m), and *Thorybes mexicana* (1430 m). The usefulness of butterflies as "zonal indicators" is questionable when some species show the zones moving upslope, others down.

Several special cases deserve individual mention.

Phyciodes campestris. - The distinctive Sierran entity *montana* does not seem to occur north of Yuba Pass. Already in Plumas County and through the Lassen, Bartle, Eddy and Trinity regions it is replaced in similar habitats - montane to subalpine meadows - by nominate *campestris*, which extends thence north to Alaska with almost no phenotypic change. *Campestris* from near Bartle are rather aberrant, but Trinity-Eddy material grades insensibly into coastal low-altitude *campestris*, which in turn grades into the spring phenotype of Central Valley *campestris* (although the summer phenotype is distinctive). We do not understand the restriction of *campestris* to the valley floor and lower foothills and its complete replacement from 1450 m upslope by *montana* (after a band some 1000 m wide in which neither occurs). We have taken female *campestris* several times between 1000 and 1500 m on the west slope and therefore assume that colonization is possible. Shapiro (1975) thought that the proportion of fully-patterned *montana* was higher at 1500 than at 2100 m, suggesting gene flow, but statistical analysis of very long series has revealed no difference in males and a significantly *lower* incidence of dark females at 1500 m (Shapiro, unpublished). The genetic relationships among the various entities in this complex badly need to be determined.

The genus *Thorybes.* - We have taken *T. pylades* and *T. m. aemilia* together at Morris Meadow and *T. m. aemilia* and *T. diversus* together at Mumford Meadow. In the Sierra Nevada these three species are "stacked" altitudinally and segregated by habitat: *T. pylades* in foothill riparian, *T. diversus* in small openings in mid-elevation montane confiferous forest, and *T. m. nevada* in high-montane to subalpine meadows. The "telescoping" referred to by Hemphill is evident here.

Anthocharis sara. - In both the Sierra and the Coast Ranges nominate *sara* occurs in foothill (mostly riparian canyon) and lower montane habitats to about 1500 m. In the higher montane and subalpine environments and on the east slope of the Sierra occurs the yellow "subspecies," *stella.* The relationship between these two is unclear. Yellow females (but not males) occur rarely in Coast Range and Sierra foothill populations. The two forms do not seem to intergrade at mid-elevations, but they do occur sympatrically or at least parapatrically; no one has reported crossing them in the laboratory. *Stella* is one more Sierran element absent from the Trinity-Eddy region presumably for historical reasons, even though seemingly suitable habitats are available. Nominate *sara* does not move up into these habitats to replace it. In this case zonal adaptation is unexpectedly strong at the "subspecies" level.

Altitudinal "Ecotypes." - In the genera *Everes, Lycaeides,* and *Apodemia,* and possibly others as described below, species occur disjunctly in different habitats at different elevations within the Trinity-Eddy region. *Everes anyntula* has at least three different hosts which occur in widely differing habitats - from streamsides in lower montane coniferous forest to the bleak, windswept alpine wastes atop Mount Eddy. There is an alpine *amyntula* on Castle Peak as well, using the same host plant (*Astragalus whitneyi*) (Shapiro, 1977). A quantitative comparison of spot-patterns for series of over 60 each of the two alpine populations shows significant differences between them, as also between each and its nearest montane population. We have been uable to partition the variation between environmental and genetic factors as yet (Shapiro, unpublished). Our series of alpine Trinity-Eddy *Lycaeides argyrognomon* is too small for statistical treatment, but there is a suggestion of phenotypic differences from montane ones. There is a definite phenological difference between the subalpine-alpine *Astragalus* feeders and the bog-meadow *Lotus* ones, and the situation is complicated by the fact that the region lies in the blend zone between the Sierran and Oregonian subspecies, *anna* and *ricei*. In the central Sierra (Carson, Sonora Passes) occur alpine *Lycaeides* on *A. whitneyi* which are phenotypically very close to *L. melissa inyoensis* but which are said to be genitalically members of the *argyrognomon* complex (P. Opler, *pers. comm.*). They do not at all resemble the montane *anna* 1000 m lower, although their ecological relationship is precisely analogous to the Trinity situation. We have determined that the *melissa*-type animal which co-occurs with *argyrognomon* on Packer's Peak and Gumboot Butte is *melissa melissa* and not distinguishable from the multivoltine, weedy *melissa* in Scott Valley, but the genetic relationship between these two is unknown.

Apodemia mormo has phenotypically indistinguishable populations on two widely different *Eriogonums* in the foothill canyons and the subalpine ultrabasic Red Trinities. The latter occur as high as any in the Sierra Nevada, where subalpine *mormo* are confined to the east slope. *Satyrium californica, sylvinus* and *saepium* all occur high in the Trinities and presumably have different hosts at different elevations. All are reported higher in the Trinity-Eddy region than in Yosemite, but all three occur at 2100 m at Donner Pass.

Euchloe ausonides is poorly understood in montane California. In both the Trinity-Eddy region and the Sierra Nevada there are high-altitude populations which are phenotypically different from lower ones, and closer to the Rocky Mountain *coloradensis*. None of these have been hybridized. Strinkingly, in the European *ausonia* the same altitudinal "subspeciation" occurs, with the entities parapatric (Higgins and Riley, 1970, p. 51 and map 23).

Atalopedes campestris. - This is usually considered an "Upper Sonoran" butterfly, resident in the hot Central Valley and lower foothills. It has bred sporadically as high as 1500 m on the Sierran west slope, and turns up as a rare stray at 2100 m (Shapiro, unpublished). MacNeill (in Howe, 1975) describes its range as "Atlantic to the Pacific in the southern half of the United States." We were quite surprised to find it in a small collection made by S. K. Peoples in Scott Valley in September 1977. In September 1979 we took it in large numbers on Rabbitbrush at Callahan and French Creek. It is a strange animal to find side-by-side with *Pieris occidentalis* and *Speyeria coronis simaetha*, once again illustrating that zonal classifications tend to break down in the arid Great Basin influence.

Competitive Interactions

Many ecologists view communities as structured by competition in both ecological and evolutionary time. In ecological time interspecific competition may exclude species from part or all of the contested resources, and hence the range (Hardin, 1960). In evolutionary time it is theorized to act by "character displacement" (Brown and Wilson, 1956) - a hypothetical process of increasing divergence of ecological requirements through time, lessening competition and permitting coexistence (and thereby packing species densely onto resources). "Character release" is the term given to the broadening of a species' resource utilization which is alleged to occur in the absence of competitors. The two phenomena are conceptually distinct but in practice may be indistinguishable if historical inferences about dispersal and sympatry cannot be made. Character displacement has become a central dogma of ecological theory (Diamond, 1978) but is not without its critics (Birch and Ehrlich, 1967; Grant, 1972; Wiens, 1977; Shapiro, 1978a). Its applicability to phytophagous insects is unclear, because their populations may be regulated by other factors before competition becomes limiting (Hairston, Smith and Slobodkin, 1960; Ehrlich and Birch, 1967). The pitfalls of applying the model in a facile way to apparent "resource partitioning" were noted by Shapiro and Carde (1970) and Carde, Shapiro, and Clench (1970).

Faunal differences like those between the Sierra Nevada and Trinity-Eddy region provide potential opportunities to test these ideas. In particular, the altitudinal compression of *Thorybes* species and *Phyciodes campestris* - *montana* situation seem interesting. In order to apply the character displacement model it is necessary, but not sufficient, to establish the identity of the resources for which the organisms compete. Habitat selection can be the evolutionary consequence of physiological limitations rather than competition, but the physiological limitations themselves might be a secondary consequence of competition. If *Anthocharis sara stella* was never in the Trinities, the failure of *A. s. sara* to expand into its habitat cannot be due to character displacement *in situ*. It could be the consequence of previous character displacement if Trinity *sara* are derived from the Sierra and are physiologically and behaviorally conservative, but there is absolutely no reason to believe this.

Another problem is the uneven distribution of phytophagous insects over potential host plants (Ehrlich and Raven 1965, Southwood 1961). The usual explanation of this is coevolutionary, based on secondary plant chemistry, but "architectural" hypotheses are now appearing (Lawton, 1978). In both the Sierra Nevada and Trinity-Eddy regions certain plants seem overloaded. The genus *Eriogonum*, used by so many Lycaenidae, is one; the legume *Astragalus whitneyi* is another. This has three blues each in two alpine faunas (*E. amyntula, L. melissa, L. argrognomon* in the Trinities; *E. amyntula, P. shasta, L. "melissa"* in the Sierra - we have not found all 3 together) while sympatric *Astragalus* are apparently ignored. The origin and organization of such densely-packed faunas should be of great interest.

The phenomena we have been discussing all disappear readily when distributions are interpreted zonally and species are treated as interchangeable. Miller (1951) addresses the problem sagaciously: "Efforts to develop broad distributional principles and categories commonly run beyond the facts and violate the essentially statistical character of distributional data. There is an urge to create simplified concepts, perhaps unwittingly as paths of least intellectual resistance. These may become lines of escape from exhaustive factual comprehension....(an) account of affairs, species by species, with its data on the habitat and distributional limits of each, may be a more substantial scientific record than (a) generalized review..."

Phenology

One of us (AMS) has carried out detailed phenological studies along an altitudinal transect parallel to Interstate Highway 80 since 1972. The data thus obtained are not strictly comparable with our Trinity-Eddy data because the former were taken by repeated intensive sampling at fixed study sites, while the latter are extensive and sporadic. We do not have enough replicates for any single Trinity site to construct a reliable seasonal species curve for it. Instead we have pooled data for the range as a whole (table 5). These are based on 1976, the year of our most wide-ranging surveys. We will defer detailed comparisons with the Sierran faunas until a later publication, but wish to comment on one unusual aspect of Trinity-Eddy butterfly phenology - the autumn "boom."

In the Mediterranean climates of California the great bulk of univoltine species occur early in the season, when soil moisture is still high for plant growth. Throughout temperate North America there is an apparent shortage of autumnal univoltines (Shapiro, 1975a). At Donner Pass in the northern Sierra there are three in a fauna of 102 species: *Apodemia mormo, Ochlodes sylvanoides,* and *Neophasia menapia.* All of these fly in September; Emmel and Emmel (1962), who stopped collecting in mid-August, missed the first two altogether. Despite this small number of univoltine species, the total number of butterflies flying at Donner in September and into early October is high, including *Polygonia zephyrus, Vanessa annabella, virginiensis,* and *cardui, Speyeria mormonia arge, S. zerene, S. coronis snyderi, Satyrium saepium, Pieris occidentalis, Hesperia juba,* and the weedy multivoltines *Colias eurytheme, Precis coenia, Plebeius acmon,* etc. (Shapiro, 1978b). Many of these same species can be collected in the Great Basin at similar seasons. In the high country and on the east side there is only one major nectar source this late in the year: Rabbitbrush, *Chrysothamnus nauseosus.* Apart from its many butterfly visitors, it has a large pollinator fauna including at least a dozen diurnal moths (mostly Noctuidae with showy, banded hindwings), Tachinid flies, and Hymenoptera. Some of these are oligolectic.

Many species emerge later in the Trinity-Eddy region than in the Sierra at similar altitudes. The autumn-univoltine fauna includes not only *A. mormo, O. sylvanoides,* and *N. menapia,* but *L. heteronea, L. arota, C. pegala boopis* (at its highest elevations), and *P. sabuleti* as well. The total butterfly biomass appears to be greatest in late September, and the best general collecting in the region, including Scott Valley, is at this time (42 species on 21 IX 79; compare 31 at Donner Pass, 10 IX and 11, 30 IX 79). The autumn "boom" includes multivoltine species like *Coenonympha tullia eryngii, Pieris occidentalis, Lycaena helloides, Lycaeides melissia,* and *Colias philodice*; females of *Speyeria zerene* and *coronis* which have emerged from adult diapause; and immense numbers of branded skippers, including *H. juba, harpalus,* and *columbia, A. campestris,* and *P. sabuleti* (which in the Trinity Alps may outnumber all other butterflies together). This autumn fauna is a Rabbitbrush fauna (along with the very similar *Haplopappus bloomeri* on ultrabasics). Without these yellow Composites it is difficult to envision the persistence of this phenology.

The most striking phenological anomaly in the Trinities is *Polites sabuleti.* The unnamed "Trinity" *sabuleti* is strictly an autumn univoltine, flying in September and early October at 1500-2000 m. In the Sierra Nevada, *P. s. tecumseh* extends from around 1400 m to above tree line; it is univoltine, with a rudimentary second brood some years in autumn at its lower limit. The flight season is progressively later with increasing elevation, so that it flies in June at 1500 m, mostly July at 2100 m, and late August and September at 3200 m plus. Thus "Trinity" *sabuleti* fly more than two months later than Sierran *tecumseh* at the same elevation, but at the same time as Sierran *tecumseh* 1700 m higher! They may be reared without diapause in the laboratory, and keep their distinctive phenotype (Shapiro, unpublished - compare Shapiro, 1975b).

We do not have appropriate climatological data to be able to say whether the unusual phenology of Trinity butterflies is due to evolved "life-history strategies" (i.e., patterns which maximize Darwinian fitness) or simply to slower degree-day accumulation working on similar physiologies. We have, however, found the coincidence of flight periods on the eastern slopes of the Sierra and in the north with the flowering time of *Chrysothamnus* to be very suggestive. *Chrysothamnus* is generally absent on the Sierran west slope, and *Haplopappus* species mostly bloom earlier; here there is little autumnal fauna except as spills over the passes. At Lang Crossing (1500 m) *N. menapia* and *A. mormo* emerge at least a month earlier than at Donner. *O. sylvanoides* flies mainly in September and virtually monopolizes *Aster*. It is by far the commonest autumn butterfly at Lang, occupying the same numerical position as *P. sabuleti* does in the Trinities (where *sylvanoides* is much less common).

Cases of potential seasonal displacements among closely-related species are rare in the Trinity-Eddy fauna. *Speyeria callippe rupestris* flies in June to mid-July; sympatric *S. atlantis, zerene,* and *hydaspe* fly together mostly from July to September *S. callippe* is also the earliest *Speyeria* on the Sierran west slope, and the one to reach the lowest elevations. It has a high larval desiccation tolerance and passes the summer as a very young larva, unlike *S. zerene* and *coronis* whose larvae are less drought-resistant, and which estivate as adults (S.R. Sims, *pers. comm.*). If this is a case of time partitioning, which is far from certain, it could reflect either competition for resources or reproductive isolation. *S. callippe* is also strikingly altitudinally allopatric with *S. egleis oweni*, a fact which may or may not be biologically significant.

Annotated List of Species

DANAIDAE

1. *Danaus plexippus* Linnaeus. Monarch.

Common throughout the Trinity-Eddy area in all open habitats, even above tree line. On 17 VI 76 a concentration of Monarchs was found around a grove of Black Cottonwoods at the upper end of Morris Meadow. Of three collected, two were worn (overwintered) males and the third was a fresh female, obviously of the spring generation. On 20 IX 79 dozens of migrating Monarchs were seen at Rabbitbrush in Scott Valley, along Interstate 5 and Highway 3. Larvae were common at 1820 m on Packer's Peak, 9 VII 77, where they had virtually defoliated the entire colony of the host plant. They are often common in Scott Valley and west to Cecilville.

HOST PLANTS: Asclepiadaceae: *Asclepias cordifolia* (Benth.) Jeps., Packer's Peak; *A. speciosa* Torr., roadsides, Callahan and Scott Valley, 29 V 77, 11 VII 77.

RECORDS: Lone Jack, 28 V 77; Cecilville, 29 V 77; lower Coffee Creek, 14 VI 80; Crawford Creek, 15 VI 80; Morris Meadow (3), 17 VI 76; Swift Creek, 25 VI 77, 1 X 76; Coffee Creek, 26 VI 77; Mt. Eddy, 6 VIII 78; Sunrise Creek, 5 IX 76; Deadfall Lakes, 20 IX 79. (28 V - 1 X)

SATYRIDAE

2. *Oeneis nevadensis* Felder and Felder. Nevada Arctic.

Common in montane coniferous forest at middle elevations. The Nevada Arctic has been found in numbers in odd years in some places and in even years in others, but thus far not in both at the same place. Adults are usually encountered sitting in sunlit spots in the forest, often on fallen logs across trails. Male-male chases are frequent but rarely long sustained. There is considerable minor variation in color and pattern.

Univoltine, with a long flight season.

HOST PLANTS: Presumably grasses, but unrecorded.

RECORDS: Boulder Creek, 12 VI 76; lower Coffee Creek (near Ranger Station), 14 VI 80; 11 km E Callahan (4), 15 VI 80; Callahan, 15 VI 80; Scott Valley, 15 VI 80; Bridge Camp, 17 VI 76; Morris Meadow (2) 17 VI 76, 26 VI 76; Lone Jack (3) 18 VI 77; Little Salt Creek, 24 VI 76; Deer Creek (2) 27 VI 76; Deadfall Lakes, 6 VIII 78; Mount Eddy, 6 VIII 78; upper Caribou Lakes Trail, 10 VIII 76; Gumboot Lake, 11 VIII 76; Cecilville, Crawford Creek (S.O.M.) (12 VI - 11 VIII)

3. *Cercyonis sthenele silvestris* Edwards. Sylvan Satyr.

Frequent in montane chaparral, Oregon Oak woodland, and dry montane coniferous forest with an understory of Huckleberry Oak, Pine-Mat Manzanita, and grasses. Decidedly colonial. Local concentrations may be encountered along sunlit trails in late afternoon, but captures are infrequent since the Sylvan Satyr flies vertically up canyon walls or takes shelter in dense brush when alarmed. Univoltine, peaking late in the season.

Considerable variation is apparent in our series. Some specimens look like north Coast Range or southwestern Oregon ones, while others apprach northern Sierran foothill material. Females seem always to have a light frosting of white scales on the ventral hindwing (less pronounced than in ssp. *paulus* Edwards). This character has not been seen on males. The Hobo Gulch specimens look like miniature *pegala*, much like those figured by Dornfeld (1980, pl. 10) from Corvallis, Oregon.

HOST PLANTS: Grasses suspected.

RECORDS: Morgan Meadows (5), 12 VII 79; Hobo Gulch (2), 18 VII 77; Deadfall Lakes (7) 6 VIII 78, (16) 16 IX 78; Packer's Peak (2), 15 VIII 77; Papoose Lake trail, 30 VIII 76; Martin Gulch fork, 30 VIII 76; Dorleska Mine to Big Flat (5), 7 IX 76; Swift Creek, 1 X 76. (12 VII - 1 X)

4. *Cercyonis pegala boopis* Behr. Ox-Eyed Satyr.

Discontinuously distributed in the Trinities and thus far unknown from Mount Eddy, the Deadfall Lakes area, or Scott Valley. The three populations studied are located along streams in lower montane coniferous forest in the foothills (mostly in Yellow Pine), flying July-August; at Morris Meadow, abundant, late July-August; and extremely localized in a hillside boggy seep draining into Parker Meadow on upper Swift Creek, abundant, September-October. The last is perhaps the highest-elevation population of *boopis* known.

Very dark, with no trace of the hoary scaling on the ventral hindwing which is so characteristic of material from Mt. Shasta City in our large Parker Meadow series; but it occurs in some males and most females at Morris Meadow.

HOST PLANTS: Probably grasses.

RECORDS: Morris Meadow, 14 VII 79, (16) 4 VIII 79; Rte. 3, milepost TR47.00, 1200 m, 7 VIII 76; Douglas City (2), 29 VIII 79; seeps draining into Parker Meadow (11) 5 IX 76, (8) 1 X 76.

5. *Coenonympha tullia* near *eryngii* Henry Edwards. Northern California Ringlet.

Common and widespread at low elevations, occurring in open, dry, often disturbed sites from the foothills through the Yellow Pine belt to about 1200 m, rarely to 2100 m in the larger meadows. Especially numerous in and along the edges of Scott Valley. In the Trinities mostly single-brooded in spring, with just a few fresh emergents in fall; apparently fully double-brooded at both Deadfall Meadow and Scott Valley. We suspect that careful statistical analysis will reveal a transition from *C. t. california* Westwood in the southern foothills to *C. t. eryngii* in the Eddies and Scott Valley.

In Scott Valley and near Callahan occur Great Basin - type sedge marshes apparently suitable for *C. t. ampelos* Edwards, but repeated searching has not turned it up. In fact, no two named entities in *Coenonympha* appear to be sympatric anywhere in northern California, although strays of both *california* and *ampelos* have been found near Donner Pass.

HOST PLANTS: Not certainly known; associated with introduced, weedy *Bromus* spp. (Granineae) on both sides of the range, but this could reflect habitat selection rather than host preference.

RECORDS: Coffee Creek (4), 27 V 77; Canyon Creek (8), 28 V 77; Lone Jack, 28 V 77; Cecilville (5), 29 V 77; Crawford Creek (2), 29 V 77, (3) 15 VI 80; Shadow Creek (2), 29 V 77; Scott Valley (11), 29 V 77; lower Coffee Creek, 14 VI 80; Eagle Creek, 14 VI 80; Callahan, 15 VI 80; Bridge Camp (2), 17 VI 76; Morris Meadow, 26 VI 76; 3.2 km W Gazelle (3), 5 VII 80; Scott Mountain summit (2), 11 VII 77; Douglas City (3), 29 VIII 79; Deadfall Meadow (7), 20 IX 79; French Creek (Scott Valley) (3), 21 IX 79; Callahan, 21 IX 79, 25 IX 77; Parker Meadow, 1 X 76 (27 V - 1 X)

NYMPHALIDAE

6. *Speyeria cybele leto* Behr. Leto Fritillary.

Recorded on the "east flank of Mount Eddy" by K. Hansen, *teste* S. O. Mattoon. Occasionally common near Mt. Shasta City. This species often turns up far from breeding habitat, so until a definite population is located within the study area its status will remain uncertain. July-September.

7. *Speyeria atlantis* near *dodgei* Gunder. Dodge's Fritillary.

This fritillary is common at mid-elevations in montane coniferous forest, often visiting Pennyroyal (*Monardella*) flowers or, late in the season, straying into more open sites where *Chrysothamnus* or *Haplopappus bloomeri* are available. Phenotypically these animals are somewhat intermediate between true *dodgei* of the Cascades and Sierran *irene* Boisduval. There is considerable individual variation. Females average much darker beneath, with much more silvering, then males. A freshly emerged female was taken on Mount Eddy as late as 20 IX 79.

HOST PLANTS: Emmel and Shields report oviposition on *Viola purpurea* Kell. at Brown's Meadow, 23 VII 68. We have seen ovipositions only after the *Viola* were dried beyond recognition.

RECORDS: Morris Meadow (2), 24 VI 76, (2) 25 VI 76, 26 VI 76, (3) 4 VIII 79; Deer Creek, 27 VI 76; Granite Creek (3), 30 VII 76; Gibson Meadows, 30 VII 76; Stuart Fork below Sawtooth Ridge (7), 5 VIII 79; Deadfall Lakes (2), 6 VIII 78, (2) 16 VIII 79, (7) 27 VIII 79, (8) 16 IX 78, (4) 20 IX 79; Mount Eddy (2) 6 VIII 78, 20 IX 79; cirque above Josephine Lake, 8 VIII 76; Caribou Lakes Trail (4), 10 VIII 76; Gumboot Lake, 11 VIII 76; lower Grizzly Meadows, 27 VIII 76, Dead Mule Camp, 5 IX 76; Union Creek Trail (7), 6 IX 76; Big Flat, 8 IX 76; Parker Meadow, 1 X 76. (24 VI - 1 X)

8. *Speyeria coronis* near *simaetha* dosPassos and Grey. Simaetha Fritillary.

Rather rare. Like *S. cybele leto*, this is a highly vagile species, especially females in autumn. It is often common in Plumas and Lassen Counties on the east slope of the Sierra and occurs at Mount Shasta City. It visits *Haplopappus, Chrysothamnus, Aster,* and other fall Composites and also *Monardella*; its light ground color and very strong silvering make it distinctve even on the wing. It prefers open, dry sites, usually near streams. Our material is smaller and lighter than ssp. *snyderi* Skinner from the Sierra Nevada.

HOST PLANTS: Unknown. Presumably violets.

RECORDS: 6.5 km W Callahan, 15 VI 80; 3.2 km W Gazelle, Robertson Ranch, 5 VII 80; Caribou Lakes Trail, 20 VII 68 (Emmel and Shields); Mount Eddy, 6 VIII 78; Packer's Peak (2), 15 VIII 77; Deadfall Lakes, 16 VIII 79, (2) 20 IX 79; Callahan, 20 IX 79. (15 VI - 20 IX)

9. *Speyeria zerene conchyliatus* J. A. Comstock. Zerene Fritillary.

This richly-colored Fritillary is not very common in the Trinities, but females swarm by dozens on Rabbitbrush in Scott Valley in fall. In the montane coniferous forest belt it generally occurs in clearings and along trails, often in the company of the Pine White, Sandhill Skipper, and other species of *Speyeria*. Trinity specimens are mostly quite similar to the well-known ones from Anthony Peak on the east side of the North Coast Ranges, but Scott Valley ones are more ochreous above and less ruddy beneath.

HOST PLANTS: Undetermined; presumably violets.

RECORDS: Crawford Creek, 15 VI 80; 11 km E Callahan, 15 VI 80; Gulick Creek, 10 VII 77; Morgan Meadows (4), 12 VII 79; Caribou Lakes Trail, 10 VIII 76; vicinity of Big Flat (3), 7 IX 76; Deadfall Lakes, 16 VIII 79, 27 VIII 79, 16 IX 78, 20 IX 79; Callahan (4), 21 IX 79; French Creek (Scott Valley) (8), 21 IX 79. (15 VI - 21 IX)

10. *Speyeria callippe rupestris* Behr. Ruddy Silver-Spot.

With *S. egleis oweni*, this is the commonest Fritillary in the Trinity-Eddy area. It is also the earliest to emerge and is seldom collected after mid-July. It occurs along the edges of meadows and along trails and streams in montane coniferous forest, from foothill canyons to about 1800 m. It visits Pussy Paws (*Spraguea*), *Monardella*, and mud puddles.

Quite variable. To the east and north, transitional specimens to ssp. *elaine* dosPassos and Grey are occasionally found. One melanic male was taken at Packer's Peak, 9 VII 77.

HOST PLANTS: Not Determined; presumable *Viola*.

RECORDS: 11 km E Callahan (5), 15 VI 80; Callahan, 15 VI 80, 6.5 km W Callahan (2), 15 VI 80; Crawford Creek (2), 15 VI 80; Willow Creek (2) 16 VI 76; Morris Meadow (5), 17 VI 76, (4) 24 VI 76, (5) 26 VI 76; Lone Jack, 18 VI 77; Stuart Fork below Sawtooth Ridge (4) 24 VI 76, 25 VI 76, (2) 5 VIII 79; Deer Creek (3), 27 VI 76; Mumford Meadow (3) 25 VI 77; Coffee Creek, 1400 m (3), 26 VI 77; Packer's Peak trail (3), 9 VII 77; Morgan Meadows, 12 VII 79; Hobo Gulch (3), 18 VII 77; Deadfall Lakes (2), 27 VIII 79; Big Flat, 7 IX 76. (15 VI - 7 IX)

11. *Speyeria egleis oweni* Edwards. Owen's Silver-Spot.

Very common to abundant at higher elevations throughout the area. There is a gentle east-west cline; Mount Eddy specimens are more contrasty, with a more olivaceous ground color, especially in females, and a paler, more contrasting disc. These characters are developed still further on the south slope of Mount

Shasta. Trinity Alps *egleis* look more like the nominate Sierran subspecies, with which they do not exchange genes directly - this presumably represents parallel variation. Although all our series are variable, they do not approach the complexity of material from Westwood, Lassen County, and the very dark forms encountered there are completely absent.

This is our only Fritillary that hilltops regularly - even above tree line on Mount Eddy and on the bare granite of the high Trinities. Here it occurs with *Parnassius phoebus sternitzkyi* and *Pieris occidentalis*. Lower, it occurs in meadows and clearings in the upper montane coniferous forest. Its altitudinal range, 1500--2750 m, barely overlaps the preceding *S. callippe rupestris*. Its flight season is long. It visits flowers freely, especially *Monardella* and *Haplopappus*.

At Deadfall Lakes males average very small and flock to mud puddles. They are easily mistaken for *S. mormonia*. Trinity-Eddy *egleis* are much more ecologically versatile than their Sierran cousins, expanding their range into moist sites of the type occupied by *S. mormonia arge* Strecker in that range. We initially thought *mormonia* was absent from the area and that we were observing the phenomenon of ecological character release, but see under *S. mormonia* below.

HOST PLANTS: Unrecorded, but presumably on violets. (*Viola purpurea* Kell.?-J.Emmel.)

RECORDS: Stuart Fork below Sawtooth Ridge, 25 VI 76; Packer's Peak summit (4), 9 VII 77; Morgan Meadows, 12 VII 79; Deadfall Lakes (3), 12 VII 79, 6 VIII 78, (15) 16 VIII 79, (8) 16 IX 78, (7) 20 IX 79; Sunrise Pass (9), 10 VII 77, 5 IX 76; Mount Eddy (3), 6 VIII 78, (5) 16 VIII 79, 27 VIII 79, 16 IX 78; Packer's Peak Trail, (4) 15 VIII 77; Caribou Lakes Trail (11), 10 VIII 76; Gumboot Butte (11), 11 VIII 76; Upper Grizzly Meadows (2), 27 VIII 76; Gulick Creek (4), 5 IX 76; Dead Mule Camp, 5 IX 76; Dorleska Mine (6), 7 IX 76; Big Flat, (4) 7 IX 76, 30 IX 76. (25 VI - 30 IX)

12. *Speyeria hydaspe purpurascens* Henry Edwards. Purplish Silver - Spot.

Common in montane coniferous forest and at the edges of mid-elevation meadows, visiting *Monardella* with the other Fritillaries. Although our series includes a great deal of individual variation, there are no geographic trends apparent. The flight season is longer and the population density higher than for *hydaspe* in the northern Sierra Nevada.

HOST PLANTS: Undetermined; presumably *Viola*. (*V. sheltonii* Torr.?-J. Emmel.)

RECORDS: Morris Meadow (2) 17 VI 76, (2) 24 VI 76, (3) 4 VIII 79; Deer Creek (2), 27 VI 76; Mumford Meadow, 25 VI 77; Packer's Peak Trail, 9 VII 77; Gulick Creek, 10 VII 77; Morgan Meadows (4), 12 VII 79; Hobo Gulch (4), 18 VII 77; Stuart Fork below Sawtooth Ridge (2), 5 VIII 79; Caribou Lakes Trail (6), 10 VIII 76; Union Creek Trail (2), 6 IX 76; Big Flat, 7 IX 76, 8 IX 76; Deadfall Lakes, 20 IX 79. (17 VI - 20 IX)

13. *Speyeria mormonia erinna* Edwards. Erinna Silver - Spot.

This was one of the great surprises of the survey. *Speyeria mormonia* is otherwise known only from the Sierra Nevada (*arge* Strecker, Yuba Pass south) and the Warner Mountains of Modoc County (? ssp.). *S. m. erinna* was previously known only from the east slope of the central Oregon Cascades. A single fresh male was taken on the uppermost grassy bog at Deadfall Lakes, 16 IX 78. A second male was taken at Deadfall Meadow on 27 VIII 79 (M. Mullins) and a female the same day on a hillside meadow-seep north of the lower Deadfall Lakes (W. Patterson). All of these lie outside the range of variation of Sierran *arge*. Because small *egleis* are so common in the Deadfall Lakes area, this butterfly is very easy to overlook. A careful search on 20 IX 79 in all the meadows failed to turn it up. Since we have large, essentially random collections of Fritillaries from the Trinities in autumn we feel confident that *mormonia* is restricted to the Deadfall Lakes - Mount Eddy part of our study area. The boggy meadow at Scott Mountain Summit, which is ecologically similar to Deadfall Meadow, should be checked slightly earlier in the season. J. Emmel suspect *Viola adunca* Sm. as the host plant. This species occurs at Deadfall and on Scott Mountain.

14. *Boloria epithore* near *chermocki* Perkins and Perkins. Chermock's Meadow Fritillary.

The Meadow Fritillary is common and generally distributed in wet meadows and bogs throughout the Trinity - Eddy area, and occasionally in drier places. Its elevational range is mostly 1200--2100 m. It usually flies with *Phyciodes campestris, Chlosyne hoffmanni segregata, Agriades glandon,* and *Thorybes mexicana aemilia*. Trinity - Eddy specimens are larger and less heavily patterned than northern Sierran ones.

HOST PLANTS: Again, presumably *Viola*. (*V. glabella* Nutt.? - J. Emmel.)

RECORDS: Boulder Creek, 12 VI 76; Mumford Meadow (2), 14 VI 76, (6) 25 VI 77; Parker Meadow, 14 VI 76; lower Bear Basin Meadow, 15 VI 76; Deadfall Meadow, 15 VI 80; Deer Creek, 16 VI 76, 27 VI 76; Willow Creek, 16 VI 76; Morris Meadow, 17 VI 76, (2) 24 VI 76; Emerald Lake, 25 VI 76; Gulick Creek, 10 VII 77; Deadfall Lakes (4), 12 VII 79, 16 VIII 79; Morgan Meadows (3), 12 VII 79; Gibson Meadow (2), 30 VII 76; Deadfall Meadow to lower Deadfall Lakes, 6 VIII 78. (12 VI - 16 VIII)

15. *Chlosyne leanira* Felder and Felder. Leanira Checkerspot.

Recorded from Crawford Creek (S.O.M. and 15 VI 80). Otherwise unrecorded from the region.

16. *Chlosyne palla* Boisduval. Northern Checkerspot.

A very common species from the foothills to about 1500 m, overlapping the next species altitudinally and in habitat. It prefers open, xeric sites, often on rocky slopes or at the foot of a cliff; it visits Pussy Paws (*Spraguea*) at the edges of dry montane meadows. Higher-elevation specimens tend to lose the black pattern, as is also observed in the Sierra Nevada. Most females are the dark form (*eremita*), with some intermediates and few fully light ones. A melanic male was taken on upper Stuart Fork, 24 VI 76, and minor "aberrations" are frequent.

HOST PLANTS: Probably Compositae. Suspect genera are *Aster, Senecio,* and *Solidago*.

RECORDS: Canyon Creek (3), 28 V 77; Scott Valley, 29 V 77, 15 VI 80; Shadow Creek, 29 V 77; Cecilville, 29 V 77; Boulder Creek, 12 VI 76; Eagle Creek (11), 14 VI 80; lower Coffee Creek (2), 14 VI 80; Crawford Creek (4), 15 VI 80; Callahan 15 VI 80; 6.5 km W Callahan, 15 VI 80; Morris Meadow, 17 VI 76, (2) 24 VI 76, (4) 26 VI 76; Lone Jack, 18 VI 77; Bridge Camp (2), 18 VI 76; Stuart Fork below Sawtooth Ridge (2), 24 VI 76; Coffee Creek, 26 VI 77; Deer Creek (6), 27 VI 76; Hobo Gulch, 18 VII 77. (28 V - 18 VII)

17. *Chlosyne hoffmanni segregata* Barnes and McDunnough. Hoffmann's Checkerspot.

Very common in wet meadows and bogs, but extending to drier, open sites as well. Its range commences at about 1400 m and reaches at least 2250. The males cluster on mud puddles and may be collected ten at a time. Our entire series appears indistinguishable from Oregon Cascade material. There is no tendency to lose the outer discal pattern as in the nominate Sierran subspecies.

HOST PLANTS: Egg masses on *Aster ledophyllus* (Gray) Gray (Compositae), Caribou Lakes, 2100 m, 23 VII 68 (Emmel and Shields).

RECORDS: Emerald Lake, 25 VI 76; Sapphire Lake (3), 25 VI 76; base of Red Rock Mountain and Gulick Creek area (13), 10 VII 77; Deadfall Lakes (4), 12 VII 79, (6) 6 VIII 78; Grizzly Meadows (10), 19 VII 77; Granite Creek, 30 VII 76; Caribou Basin, 23 VII 68 (Emmel and Shields), 9 VIII 76. (25 VI - 9 VIII)

18. *Euphydryas chalcedona* Doubleday. Chalcedon Checkerspot.

(a) *foothill populations*

The large foothill-canyon members of this complex do not seem phenotypically different from northern Coast Range specimens, except for a tendency for the median band to be clouded with red-resembling in this regard mid-west-Sierran-slope "*truckeensis* Gunder" rather than the very red bog-meadow populations (*dwinellei* H. Edwards, *sperryi* Chermock and Chermock) from near Bartle, Siskiyou County. We have reared four south-slope Trinity larvae. All lacked the white stripes of *truckeensis*, thus resembling Coast Range larvae.

Males patrol stream edges and roadsides and perch both on the ground and on tall plants. Male-male chases are frequent and prolonged. The more secretive females fly but little, but can be collected from Yerba Santa flowers with the males.

HOST PLANTS: Four larvae collected at Lone Jack, 28 V 77, from an undetermined shrubby *Penstemon* (Scrophulariaceae), were reared on *Plantago* and eclosed in late June-early July.

RECORDS: Coffee Creek, 850m, (4) 27 V 77, 14 VI 80; Coffee Creek, 1400 m, (18) 14 VI 80, (5) 26 VI 77; Lone Jack (2), 28 V 77, (5) 18 VI 77; Cecilville (2), 28 V 77; Crawford Creek (9), 15 VI 80; 6.5 km W Callahan (3) 15 VI 80; 11 km E Callahan (9), 15 VI 80. (27 V - 26 VI; based on rearing, perhaps extending to mid VII)

(b) *subalpine populations*

All our subalpine *Euphydryas* from the granite Trinities appear to be *chalcedona*. Most are quite red, but there is considerable variation and one male from Packer's Peak (where *chalcedona* co-occurs with *editha, q.v.*) is almost as black as foothill ones.

Common on granite scree, occasional on ultrabasics and metamorphics; males course up and down unstable, barren slopes, rarely if ever visiting flowers, and are difficult to net. They are highly territorial, displaying a mixture of perching and patrolling behavior. Females are much less often seen than males; ours are very red. We are unable to assign these populations to any subspecific name at this time.

HOST PLANTS: Emmel and Shields report two *chalcedona*-type egg masses on *Penstemon newberryi* ssp. *berryi* (Eastw.) Keck at Caribou Lake, 23 VII 68. This is one of several common high-altitude *Penstemon* (Scrophulariaceae) in the Trinities (Ferlatte, pp. 135-138). At Packer's Peak, where both *Euphydryas* occur, there are three *Penstemon: davidsonii* Greene, *purpusii* Bdg., and the rare, endemic *tracyi* Keck - but not *newberryi*. Larvae and host records are urgently needed.

RECORDS: Sapphire Lake (2), 25 VI 76; Packer's Peak, 9 VII 77; base of Red Rock Mountain, 10 VII 77; Granite Lake, 31 VII 76; Emerald Lake, 5 VIII 79; Stuart Fork below Sawtooth Ridge, 5 VIII 79; cirque above Josephine Lake, 8 VIII 76; Caribou Basin, 22 VII 68 (Emmel and Shields), (2) 9 VIII 76, 10 VIII 76. (25 VI - 10 VIII)

19. *Euphydryas editha* Boisduval. Editha Checkerspot.

(a) *foothill populations*

S. O. Mattoon has collected low-elevation *editha* near Crawford Creek and describes them as "near *edithana* Strand," a northeastern California subspecies. According to M. Singer (*pers. comm.*) this population belongs to a *Collinsia*-feeding group (Scrophulariaceae).

(b) *subalpine population* (near *colonia* Wright?)

So far this entity has been found only on Packer's Peak, where it flies with subalpine *chalcedona* over bare scree. It is very red, but there is extensive individual variation as is common with *editha*. We have searched unsuccessfully for subalpine *Euphydryas* on Mount Eddy, which is ecologically similar to the Red Trinities and Packer's Peak.

RECORDS: Packer's Peak (10), 9 VII 77.

20. *Phyciodes campestris campestris* Behr. Field Crescent.

The biogeographic independence of the Trinities from the Sierra is underscored by the absence of *P. c. montana* Behr, the light-colored montane subspecies of the Sierra, and its ecological replacement by nominate *campestris* which in the Sierra occurs in the foothills and from Yuba Pass north. The Field Crescent has been taken in the Trinity-Eddy area from foothills to about 2400 m. It is commonest in bogs and boggy meadows at 1500-2100 m, where its very long flight season indicates at least a partial second brood (in the Trinities, but perhaps not on Mount Eddy). Males fly swiftly over open, sedgy areas. Females are often seen at flowers, especially various asters.

Nominate *campestris* ranges north to Arctic Alaska. It shows great phenotypic constancy over this vast region, although breaking into races in the Central Valley and southward.

HOST PLANTS: Compositae: *Aster ledophyllus* Gray (Gray) and *A. alpigenus* (T. and G.) Gray ssp. *andersonii* (Gray) Onno are both strongly suspected.

RECORDS: Parker Meadow (2), 14 VI 76, 5 IX 76; Willow Creek, 16 VI 76; Lone Jack, 18 VI 77; Morris Meadow, 24 VI 76; Mumford Meadow (17), 25 VI 77, (3) 5 IX 76; Deer Creek (7) 27 VI 76; Packer's Peak Trail, 9 VII 77; Gulick Creek (6), 10 VII 77; Scott Mountain Summit (3), 11 VII 77; Granite Creek, 30 VII 76; Deadfall Lakes (6), 12 VII 79, (4) 6 VIII 78, 27 VIII 79; Morgan Meadows (11), 12 VII 79; Granite Lake trail (4), 31 VII 76; Mount Eddy (10), 6 VIII 78; cirque above Josephine Lake, 8 VIII 76; Big Flat, 7 VIII 76; Dead Mule Camp (2), 5 IX 76; Union Creek Trail, 6 IX 76; Swift Creek (3), 1 X 76. (14 VI - 1 X)

21. *Phyciodes orseis orseis* Edwards. Orseis Crescent.

A rare, little-known species. Recorded at one locality in our survey and independently at the same locality by S. O. Mattoon. Flies along a sunlit stream in lower montane coniferous forest, with *Phyciodes mylitta, Papilio eurymedon, Parnassius clodius, Everes amyntula,* and *Pieris napi*. It is easily overlooked due to its similarity to the two common *Phyciodes*, with which it often flies. A number of California collectors have mistakenly classified large, richly colored female *P. campestris* as this species. Such females are especially common in Siskiyou County. More data on the ecological requirements of *P. o. orseis* are urgently needed.

On 26 VII 80 two males were taken on Deadfall Meadow among large numbers of *P. campestris*; both were fresh. This represents not only a range extension and a late seasonal record, but the highest elevation record for the species (2100 m +). *Cirsium breweri* is present.

HOST PLANTS: Not known locally, but *Cirsium breweri* (Gray) Jeps. (Compositae) is present in the habitat. (*C. cymosum* (Greene) Howell occurs on the higher slopes.)

RECORDS: Crawford Creek (2), 29 V 77, 15 VI 80. (S.O.M. has additional records.)

22. *Phyciodes mylitta* Edwards. Mylitta Crescent.

Although the Mylitta Crescent is one of the commonest "weedy" butterflies on the Pacific Slope, it occurs in an unusual and restricted habitat in the Trinities - the mid-elevation bogs on serpentine drainages. Here it is locally common and double-brooded, feeding on a native thistle restricted to this habitat. Occasional specimens turn up in a variety of situations at lower elevations. It is possible that the smaller foothill and larger bog phenotypes represent genetically distinct entities, but specimens resembling Trinity bog ones do turn up elsewhere, mostly in late spring. The phenotype may simply reflect development on high-quality hosts. An extreme aberration of bog *mylitta* was taken 25 VI 77 at Mumford Meadow.

HOST PLANTS: Compositae: *Cirsium breweri* (Gray) Jeps., the bog thistle, at numerous locations in the Swift Creek drainage; larvae common much of the season, often defoliating the plants; not found on *C. breweri* at Deadfall Meadow in 1979. At Lone Jack, 18 VI 77, larvae common on the European weedy thistle *Cirsium vulgare* (Savi) Tenore.

RECORDS: Canyon Creek, 28 V 77; Cecilville, 29 V 77; Shadow Creek, 29 V 77; Crawford Creek, 29 V 77, 15 VI 80; Scott Valley, 29 V 77; 6.5 km W Callahan, 15 VI 80; Callahan, 15 VI 80; Morris Meadow, 17 VI 76; Stuart Fork below Sawtooth Ridge, 24 VI 76, (2) 5 VIII 79; Mumford Meadow (11), 25 VI 77; Coffee Creek, 1400 m, (6) 26 VI 77, 7 VII 77; Deer Creek (2) 27 VI 76; 3.2 km W Gazelle (3), 5 VII 80; Gulick Creek (2) 10 VII 77; base of Red Rock Mountain, 10 VII 77; Morgan Meadows (3), 12 VII 79; Hobo Gulch (3), 18 VII 77; Grizzly Meadows (5), 19 VII 77; Granite Lake (2), 31 VII 76; cirque above Josephine Lake, 8 VIII 76; Caribou Basin (4), 9 VIII 76; Packer's Peak trail, 15 VIII 77; Deadfall Meadow, 27 VIII 79, (3) 20 IX 79; Douglas City, 29 VIII 79; Dead Mule Camp, 5 IX 79; Union Creek trail (2), 6 IX 76; Deadfall Lakes (12), 16 IX 78; French Creek (Scott Valley), 21 IX 79; Big Flat (3), 24 IX 77, 30 IX 76; Swift Creek (7), 1 X 76. (28 V - 1 X)

23. *Polygonia satyrus* Edwards. Satyr Anglewing.

Rare in the Trinity-Eddy area, but recorded twice in one locality, in a riparian Black Cottonwood grove with nettle understory, flying with *Nymphalis milberti, Carterocephalus palaemon,* and *Papilio rutulus.*

HOST PLANTS: *Urtica holosericea* Nutt. strongly suspected.

RECORDS: Crawford Creek, 15 VI 80; Coffee Creek, 1400m, 26 VI 77, 7 VII 77. All hibernators. Also reported from below Deadfall Lakes (S.O.M.).

24. *Polygonia faunus rusticus* Edwards. Rustic Anglewing.

We have only three records of this insect, in widely separated and ecologically different sites - mid-elevation riparian forest, a boreal meadow on granite with willows and Mountain Hemlock, and the dry edge of a wet montane meadow on serpentine. Two of the specimens were taken on fall Composites (*Aster* and *Solidago*).

HOST PLANTS: *Salix* strongly suspected.

RECORDS: Coffee Creek, 1400 m, 7 VII 77 (2 hibernators); Caribou Basin, 9 VIII 76 (fresh); Deadfall Lakes, 16 IX 78 (fresh).

25. *Polygonia zephyrus* Edwards. Zephyr Anglewing.

This is the only common *Polygonia* in the area, occurring from about 1400 m to tree line and above (as a hilltopper). It often visits *Monardella* in the company of *Speyeria egleis oweni*, or *Chrysothamnus* with *Neophasia menapia*; in *Parnassius phoebus sternitzkyi* country it perches on rocks, or in sunlit glades along forest trails at lower altitudes. Worn hibernators have been taken as late as mid-August (Mount Eddy) and fresh specimens as early as mid-July. Trinity-Eddy *zephyrus* are browner beneath than Sierran ones, and tend to have little or no yellow on that surface.

HOST PLANTS: In the Sierra usually reported on *Ribes*, but in the Trinity-Eddy area females have been seen repeatedly in Willow (*Salix*) thickets.

RECORDS: Bear Basin (2), 15 VI 76; Stuart Fork below Sawtooth Ridge, 24 VI 76; Swift Creek, 25 VI 77; Coffee Creek, 1400 m (2), 26 VI 77; Packer's Peak (2), 9 VII 77, (3) 15 VIII 77; Sunrise Pass (2), 10 VII 77; Deadfall Lakes (2) 12 VII 79, (3) 6 VIII 78, (2) 16 IX 78; Grizzly Meadows (2), 19 VII 77; Mount Eddy (2), 6 VIII 78, 16 VIII 79; cirque above Josephine Lake (3), 8 VIII 76; Brown's Meadow, 10 VIII 76; NW shore Grizzly Lake, 27 VIII 76; lower Grizzly Meadow, 27 VIII 76; Yellow Rose Mine Trail, 5 IX 76; Dead Mule Camp (3), 5 IX 76; Dorleska Summit, 7 IX 76; Deadfall Meadow (4) 20 IX 79; Callahan, 21 IX 79; Swift Creek, 1 X 76. (15 VI - 1 X)

(25A. *Polygonia oreas silenus* Edwards. Silenus Anglewing.

A fresh male was taken 3.2 km W Gazelle, 5 VII 80 (J. Hayes). This is the only record of this very rare species near the study area.)

26. *Nymphalis milberti Godart.* Milbert's Tortoise Shell.

Frequent to common, from 1400 m to above tree line (as a hilltopper); often at *Monardella* flowers. The biology of this species in the West is poorly understood. It seems to undergo altitudinal migrations seasonally, but such phenomena are not apparent from our Trinity - Eddy records. All our specimens are strongly yellow-banded (*subpallida* Ckll.), but a very large series from Mount Shasta Ski Bowl, 16 VIII 77, shows extensive variation in this character.

Numbers of *Nymphalis milberti* were unusually high from 1977 through 1979, not only in the study area but throughout northern California. We did not see the species in 1976 and suspect its numbers fluctuate a great deal.

HOST PLANTS: Presumably *Urtica*, as elsewhere.

RECORDS: 6.5 km W Callahan, 15 VI 80; Callahan, 15 VI 80; 3.2 km W Gazelle, 15 VI 80; Coffee Creek, 1400 m, 26 VI 77; Deadfall Lakes, 12 VII 79, 6 VIII 78, (3) 16 IX 78, 20 IX 79; Mount Eddy summit (4) 6 VIII 78; Packer's Peak summit, 15 VIII 77. (15 VI - 20 IX)

27. *Nymphalis californica* Boisduval. California Tortoise Shell.

Generally common, occasionally migratory and abundant. Montane coniferous forest, and hilltopping on summits; on 6 VIII 78 hilltoppers were seen flying over snowdrifts atop Mount Eddy. No major outbreaks occurred during the survey. During such episodes, millions of Tortoise Shells may move through Shasta Valley. Non-migratory *californica* are often seen on *Monardella*, *Haplopappus bloomeri*, and mud puddles. This is one of the few Trinity-Eddy butterflies that will fly on cold, cloudy, even rainy days.

HOST PLANTS: Rhamnaceae: A colony of larvae on 28 V 77, Canyon Creek, defoliating *Ceanothus integerrimus* var. *californicus* (Kell.) Benson.

RECORDS: Crawford Creek (2), 15 VI 80; 6.5 km W Callahan, 15 VI 80; Callahan, 15 VI 80; Morris Meadow (2), 16 VI 76; Swift Creek, 25 VI 77; Emerald Lake, 25 VI 76; Deer Creek (2) 27 VI 76; Coffee Creek, 1400 m, 26 VI 77; Packer's Peak summit, 9 VII 77; Morgan Meadows, 12 VII 79; Mount Eddy summit, 6 VIII 78; Deadfall Meadow, 20 IX 79; Big Flat, 30 IX 76. (15 VI - 30 IX)

28. *Nymphalis antiopa* Linnaeus. Mourning Cloak.

Common and general in riparian habitat, along trails through montane coniferous forest, and at edges of wet meadows; foothills to 2100 m. Hibernators live into early August, but fresh specimens have been taken in late June in the foothills and mid-August at the upper limit of the range. Spring males are highly territorial.

HOST PLANTS: Larvae abundant on *Salix jepsoni* Schneid., Coffee Creek, 4500 feet, 7 VII 77.

RECORDS: Cecilville, 29 V 77; Boulder Creek, 12 VI 76; Callahan, 15 VI 80; Crawford Creek, 15 VI 80; 6.5 km W Callahan, 15 VI 80; Lone Jack, 18 VI 77; Swift Creek, 25 VI 77; Coffee Creek, 1400 m, 26 VI 77; Deadfall Lakes, 6 VIII 78; Gumboot Lake, 11 VIII 76; Packer's Peak trail, 15 VIII 77. (29 V - 15 VIII)

29. *Vanessa annabella* Field (*carye* auct.) West Coast Lady.

Occasional (Trinities) to common (Mount Eddy) in almost any open habitat; usually on flowers - *Monardella, Chrysothamnus, Haplopappus* and *Aster* are all favorites - but sometimes seen perching in sunlit spots in trails or on streambanks, or on hilltops, usually in late afternoon. Apparently at least partially double-brooded.

HOST PLANTS: Malvaceae: *Sidalcea oregana* (Nutt.) Gray ssp. *spicata* (Regel) Hitchc. (Deadfall Lakes and Mumford Meadow, larvae).

RECORDS: Scott Valley, 15 VI 80; Mumford Meadow, 25 VI 77; Sunrise Pass, 10 VII 77; Deadfall Lakes, 6 VIII 78, (2) 16 IX 78, 20 IX 79; cirque above Josephine Lake, 8 VIII 76; Mount Eddy, 16 VIII 79; Union Creek trail (2), 6 IX 76; Dorleska Mine, 7 IX 76; Callahan, 21 IX 79. (15 VI - 21 IX)

30. *Vanessa virginiensis* Drury. American Painted Lady (Painted Beauty).

Frequent as a hilltopper; the commonest *Vanessa* at high elevations except during *cardui* migrations. Fresh specimens emerge in August and September and visit the fall Composites; perhaps only single-brooded at higher elevations.

HOST PLANTS: Compositae: *Gnaphalium palustre* Nutt., larvae, Big Flat, 15 VIII 77; *Anaphalis margaritacea* (L.) Benth., Lone Jack, 18 VI 77.

RECORDS: Deadfall Meadow, 15 VI 80; Swift Creek, 25 VI 77; Morris Meadow, 26 VI 76; Packer's Peak, 9 VII 77, (2) 15 VIII 77; Mount Eddy summit (3), 6 VIII 78; Caribou Lakes Trail, 10 VIII 76; Gumboot Butte, 11 VIII 76; Parker Creek trail (2), 6 IX 76; Dorleska Mine, 7 IX 76; Big Flat (2), 8 IX 76; Deadfall Lakes, 16 IX 78; Callahan, 21 IX 79. (15 VI - 21 IX)

31. *Vanessa cardui* Linnaeus. Painted Lady.

The Painted Lady, one of the world's most widely distributed butterflies, is irregular in its occurrence in the Trinity-Eddy area but is occasional in all open habitats from the foothills to 2700 + m. On September 20, 1979, hundreds were seen throughout the Eddies and Scott Valley, mostly feeding at flowers of Rabbitbrush (*Chrysothamnus*). These were probably migrating southward, as there had not been any large-scale breeding locally in 1979. Migrating females generally have very large fat bodies and no ripe eggs.

HOST PLANTS: Extremely polyphagous. We have one larva from *Cirsium vulgare* (Savi) Tenore, Lone Jack, 28 V 77, and numerous empty nests on this plant and *C. breweri* (Gray) Jeps. (Compositae).

RECORDS: Coffee Creek Ranger Station, 27 V 77; Mumford Meadow, 25 VI 77; Coffee Creek, 1400 m, 26 VI 77; Packer's Peak (2), 9 VII 77, (2) 15 VIII 77; Morgan Meadows, 12 VII 79; Mount Eddy summit, 6 VIII 78, (3) 16 VIII 79; Deadfall Lakes (8), 20 IX 79; Callahan, 21 IX 79. (27 V - 21 IX)

32. *Vanessa atalanta* Linnaeus. Red Admiral.

The Red Admiral seems to be rare in the Trinity-Eddy region; we have only two records. The Douglas City male was taken on a roadside Yellow Star Thistle, the Canyon Creek one in a sunny glade among Yellow Pine and White Fir. Probably largely confined to foothill riparian and lower montane coniferous forest.

HOST PLANTS: Not determined; Urticaceae elsewhere.

RECORDS: Canyon Creek, 28 V 77; Douglas City, 2 X 76.

33. *Precis coenia* Huebner. Buckeye.

Common and general. The Buckeye occurs in all the meadows up to 2300 m at least, and in a variety of other habitats as a stray or casual. Its regular occurrence at high elevations is in striking contrast to the northern Sierra, where it is only a sporadic visitor above 1500 m most years. It seems unlikely that it is a permanent resident at high elevations in either range. The shorter distance from overwintering habitats in the foothills (sharper elevational gradient) may facilitate its colonizing Trinity meadows as compared to Sierran ones.

There is extensive individual variation; as usual autumn specimens, especially females, are often strongly reddish or purplish ventrally.

Adults regularly visit Pussy Paws and various Composites, including Rabbitbrush (*Chrysothamnus*). Males often perch in trails or on bare soil, darting out at anything that moves.

HOST PLANTS: No larvae collected in our survey; Scrophulariaceae and Plantaginaceae elsewhere.

RECORDS: Mumford Meadow, 14 VI 76, 25 VI 77; Morris Meadow, 17 VI 76, 24 VI 76, 26 VI 76, 14 VII 79, 4 VIII 79; Lone Jack, 18 VI 77, Deer Creek, 27 VI 76; Packer's Peak, 9 VII 77, (2) 15 VIII 77; Hobo Gulch, 18 VII 77; Deadfall Lakes, 12 VII 79, (3) 6 VIII 78, (12) 16 IX 78, 20 IX 79; Morgan Meadows, 12 VII 79; Grizzly Meadows (2) 19 VII 77; Big Flat, 4 IX 76, (2) 8 IX 76, (3) 24 IX 77; Gulick Creek, 5 IX 76; Dead Mule Camp, 5 IX 76; Dorleska Mine (2), 7 IX 76; Callahan, 21 IX 79; French Creek (Scott Valley) (2) 21 IX 79; Swift Creek, 1 X 76; Douglas City (4), 2 X 76. (14 VI - 2 X)

34. *Limenitis lorquini* Boisduval. Lorquin's Admiral.

Common near willows, foothills to 2100 m. Males often perch on sunlit branches. Trinity-Eddy specimens are usually reddish-orange tinted beneath with extensive black areas, with little bluish-white. In this they resemble Coast Range specimens, tending toward ssp. *burrisonii* Maynard of the Pacific Northwest; Sierran specimens and those from the Central Valley are usually whitish. One female from Morris Meadow, 17 VI 76, has a complete dorsal orange spot-band on the hind wing.

Two broods below 1500 m; perhaps only one at the upper end of the range at least in some years.

HOST PLANTS: *Salix* spp. strongly suspected.

RECORDS: Lone Jack, 28 V 77, (2) 18 VI 77; lower Coffee Creek (2) 14 VI 80; Crawford Creek, 15 VI 80; 5 km W Callahan, 15 VI 80; Morris Meadow, 16 VI 76, 17 VI 76, 4 VIII 79; Mumford Meadow, 25 VI 77; Coffee Creek, 26 VI 77; Packer's Peak Trail, 9 VII 77; Granite Lake Trail, 31 VII 76; Emerald Lake, 5 VIII 79; Mount Eddy, 6 VIII 78; cirque above Josephine Lake, 8 VIII 76; Brown's Meadow, 10 VIII 76; Union Creek Trail, 6 IX 76; Deadfall Lakes, 16 IX 78; Scott Valley, 21 IX 79. (28 V - 21 IX)

35. *Adelpha bredowii californica* Butler. California Sister.

Common in the foothills and lower montane coniferous forest, where it is clearly double-brooded. Strays to 2100+ m. Males patrol roads, trails, and creek bottoms, usually near oaks. Neither sex has ever been seen on flowers in the Trinities, but taken at *Chrysothamnus* on the banks of the Scott River. There is virtually no variation in this species.

HOST PLANTS: *Quercus* spp. suspected.

RECORDS: Canyon Creek, 28 V 77; Deadfall Meadow, 15 VI 80; 11 km E Callahan, 15 VI 80; lower Coffee Creek canyon, 14 VI 80; Morris Meadow, 16 VI 76, 17 VI 76; Willow Creek (2), 16 VI 76; Lone Jack, 18 VI 77; Swift Creek, 25 VI 77, 1 X 76; Coffee Creek, 26 VI 77; Sunrise Creek, 5 IX 76; Deadfall Lakes (3), 16 IX 78, 20 IX 79; Callahan, 21 IX 79; Big Flat, 30 IX 76. (28 V - 1 X)

RIODINIDAE

36. *Apodemia mormo* Felder and Felder. Mormon Metalmark.

Like *Cercyonis pegala boopis*, this species has disjunct populations at various altitudes scattered within the study area. It also seems to fluctuate markedly in numbers from year to year. Foothill populations are associated with an *Eriogonum* of the *latifolium* group in hot, dry canyons; montane - subalpine ones, with a member of the *E. umbellatum* complex, mostly on ultrabasics. The specimens seem phenotypically identical, and are very dark and blackish. Subalpine ones fly with the Blue Copper, *Lycaena heteronea*. They visit blossoms of *Chrysothamnus* and *Haplopappus bloomeri* as well as those of the host plant. They spend a great deal of time walking about, waving their wings, and are very difficult to follow once in the air.

HOST PLANTS: (foothill) *Eriogonum nudum* ssp. *sulphureum* (Greene) Stokes at Carrville; the same plant is used in the Klamath River country farther north. (subalpine) *E. umbellatum* Torr. complex (Gulick Creek, Dorleska Mine).

RECORDS: *Foothill*: Rte. 3, milepost TR47.00, 1200 m, 7 VIII 76; Carrville, 7 VIII 76. *Subalpine*: Packer's Peak (2) 15 VIII 77; Yellow Rose Mine Trail (2) 5 IX 76; Gulick Creek (2) 5 IX 76; Parker Creek Trail and Divide (4) 6 IX 76; Dorleska Mine (10), 7 IX 76; Dorleska Summit (2) 7 IX 76; Big Flat (2), 8 IX 76; Deadfall Lakes (2) 16 IX 78, 20 IX 79 (7 VIII, 15 VIII - 20 IX)

LYCAENIDAE

37. *Lycaena arota* Boisduval. Tailed Copper.

Frequent to locally common in alder thickets by streamsides in montane coniferous forest; occasionally at edges of meadows, perching on twigs in dappled light and shade. The Tailed Copper emerges late in the season. Unlike Sierran populations, Trinity-Eddy *arota* rarely visit flowers, but we have records at *Eriogonum umbellatum, Chrysothamnus,* and *Aster*, and at mud puddles.

Variation in this species is complex. There seems to be a double cline, elevational and directional. The darkest specimens are from lower elevations in the western and southern parts of the area, the lightest from the east slope of the Trinities and the Eddies. The dark specimens resemble those from 1500 m on the Sierran west slope, while the light ones are more like those from 2100 m. All the North Coast specimens we have seen are of the dark phenotype.

HOST PLANTS: Undetermined; *Ribes* elsewhere.

RECORDS: Stuart Fork below Sawtooth Ridge (4) 5 VIII 79; Deadfall Lakes, 6 VIII 78, (5) 16 IX 78; Packer's Peak Trail (12), 15 VIII 77; Yellow Rose Mine Trail (8), 5 IX 76; Dead Mule Camp (9), 5 IX 76; Union Creek Trail (6), 6 IX 76; Dorleska Mine (3), 7 IX 76; Big Flat (5), 7 IX 76, (10) 8 IX 76; Deadfall Meadow, 20 IX 79. (5 VIII - 20 IX)

38. *Lycaena gorgon* Boisduval. Gorgon Copper.

Frequent in foothill canyons, reaching the lower montane coniferous forest and straying higher. One brood in late spring. The biology of this species in the northern mountains has received little attention. It is much commoner farther east.

HOST PLANTS: Polygonacae: *Eriogonum nudum* complex suspected.

RECORDS: Lone Jack, 28 V 77, 18 VI 77; Crawford Creek (5), 15 VI 80; 6.5 km W Callahan, 15 VI 80; Callahan (3), 15 VI 80; 11 km E Callahan, 15 VI 80; Swift Creek trailhead, 25 VI 77; slope below Grizzly Meadow, 18 VII 77. (28 V - 18 VII)

39. *Lycaena heteronea* Boisduval. Blue Copper.

The Blue Copper is very abundant in the subalpine zone, where it seldom strays more than a few m from its host plant. It prefers barren, rocky sites - reaching its greatest densities on serpentine talus and vegetated mine tailings. Females are extremely variable, ranging from light forms resembling the relict Coast Range populations to very dark ones scarcely distinguishable from the Rocky Mountain subspecies *gravenotata* Klots, and blue ones almost indistinguishable from southern California *clara* H. Edwards. Sierran populations are much less variable, and tend to have strongly yellowish females. Populations similar to ours have been found in the Yolla Bollys by S. O. Mattoon.

Males are "perchers" and return repeatedly to the same site if disturbed. Females are usually found on flowers of the host. The commonest butterfly associates are *Hesperia juba* and *Apodemia mormo*.

HOST PLANTS: Polygonaceae: *Eriogonum umbellatum* Torr. complex.

RECORDS: above Gibson Meadows, 30 VII 76; Granite Creek (3), 30 VII 76; Emerald Lake, 5 VIII 79; ledge above Josephine Lake, 8 VIII 76; cirque above Josephine Lake, 8 VIII 76; upper Caribou Lakes Trail, 1900 m, 10 VIII 76; Packer's Peak (6), 15 VIII 77, 30 IX 76; Deadfall Lakes (2) 16 VIII 79, 27 VIII 79; Sunrise Pass, 5 IX 76; Sunrise Creek (2), 5 IX 76; Gulick Creek (14), 5 IX 76; Dorleska Mine (27), 7 IX 76; Mount Eddy (2), 16 IX 78. (30 VII - 30 IX)

40. *Lycaena nivalis* Boisduval. Nivalis Copper.

Very common throughout the montane and subalpine zones, occurring at edges of dry meadows, on rocky slopes and along trails, usually in full sun; visits Pussy Paws (*Spraguea*) freely. Trinity-Eddy populations are strikingly two-toned beneath; this phenotype occurs northward into Oregon and east to the Warner Mountains but not in the Sierra Nevada. A few males have the red subterminal line above concolorous with the ground. Single-brooded, but with a very long flight season.

HOST PLANTS: Polygonaceae: *Polygonum spergulariaeforme* Meissn. very strongly suspected. This plant is much commoner and more widespread in the Trinity-Eddy region then the usual Sierran host, *P. douglassii* Greene, to which it is closely related.

RECORDS: Morris Meadow, 17 VI 76, (4) 24 VI 76, 26 VI 76; Mumford Meadow (4) 25 VI 77; Sapphire Lake (2), 25 VI 76; Deer Creek (2), 27 VI 76; Coffee Creek, 4500 feet, 7 VII 77; Packer's Peak Trail (2) 9 VII 77; Morgan Meadows (2), 12 VII 79; Grizzly Meadows (3), 19 VII 77; above Gibson Meadows, 30 VII 76; Emerald Lake, 5 VIII 79; Deadfall Lakes, 6 VIII 78, (2) 16 VIII 79, (2) 27 VIII 79, (2) 16 IX 78; Mount Eddy (3) 6 VIII 78; cirque above Josephine Lake (8), 8 VIII 76; Caribou Basin (3), 9 VIII 76; Brown's Meadow, 10 VIII 76; Union Creek Trail (3), 6 IX 76; Deadfall Meadow, 20 IX 79. (17 VI - 20 IX)

41. *Lycaena mariposa* Reakirt. Mariposa Copper.

Common in small glades and at the edges of meadows among Lodgepole Pines, at the upper end of the montane coniferous forest, and in the smaller subalpine meadows of the Caribou Basin; frequently found on flowers of *Helenium bigelovii* Gray - a plant rarely visited by butterflies - and of *Aster alpigenus* ssp. *andersonii* (Gray) Onno (both Composites). Both sexes usually sit well off the ground and can thus be told quickly from the preceding *L. nivalis* at a distance.

Trinity-Eddy specimens average more heavily marked beneath than Sierran ones from similar elevations and habitats.

HOST PLANTS: Unknown. (Rosaceae: *Horkelia* and *Potentilla* suspected in the Sierra.)

RECORDS: Scott Mountain Summit, 11 VII 77; Mount Eddy (3), 6 VIII 78, 27 VIII 79; Deadfall Meadow, 6 VIII 78, 16 VIII 79; cirque above Josephine Lake (4), 8 VIII 76; Caribou Basin (10), 9 VIII 76; upper Caribou Lakes Trail, 10 VIII 76. (11 VII - 16 VIII)

42. *Lycaena helloides* Boisduval. Purplish Copper.

This is a weedy, low-elevation species in most of California. It occurs sporadically in the southern foothills but is abundant in fall in Scott Valley, where it must be double-brooded. In the Trinities and Eddies it occurs sporadically but can be locally common, suggesting temporary local breeding. Autumn adults visit flowers of *Aster* and *Chrysothamnus*.

HOST PLANTS: Unknown locally, but both *Rumex crispus* and *R. acetosella* (Polygonaceae) are common in Scott Valley; the former occurs along Coffee Creek road and the latter is a widespread montane weed.

RECORDS: Coffee Creek, 850 m (5) 27 V 77, 14 VI 80; 3.2 km W Gazelle, 15 VI 80, 5 VII 80; 6.5 km W Callahan, 15 VI 80; Callahan, 15 VI 80, 21 IX 79; Mumford Meadow (2), 25 VI 77; Coffee Creek, 1400 m, (3) 26 VI 77; Morris Meadow, 14 VII 79; Packer's Peak trail, 15 VIII 77; Deadfall Lakes (10), 16 IX 78, 20 IX 79; Edgewood, 20 IX 79; French Creek (Scott Valley) (9), 21 IX 79. (27 V - 21 IX)

(42A. *Lycaena editha* Mead. Edith's Copper.

Occurs 3.2 km W Gazelle, B. Robertson ranch, 5 VII 80. Unrecorded in study area.)

43. *Habrodais grunus* Boisduval. Canyon Oak Hairstreak.

Common on dry slopes in montane chaparral, and in hot foothill canyons, wherever Canyon Oak (Goldencup Oak), *Quercus chrysolepis*, grows; also found once with *Q. vacciniifolia*, but never with *Q. garryana*. The butterflies sit in the oaks, from which they may be startled with a net, but do not visit flowers. They are most

active in late afternoon, when multiple male - male chases are common. One brood, flying in late summer. There is considerable variation, from quite light (mostly east slope and Mount Eddy) to dark (south slope of Trinities; resembles Coast Range material). We were surprised to find this species so common to such high elevations, as it rarely goes over 1500 m in the mid-Sierra, and then only in the most xeric sites.
HOST PLANTS: Fagaceae: *Quercus chrysolepis* Liebm. (slope above Big Flat); possibly also *Q. vacciniifolia* Kell. (Sawtooth Ridge).
RECORDS: Hobo Gulch (4), 18 VII 77; Granite Creek, 30 VII 76; Deadfall Lakes (4), 6 VIII 78, (6) 16 IX 78; south slope Sawtooth Ridge, 2000 m, 8 VIII 76; Packer's Peak Trail (4) 15 VIII 77; Bob's Farm, 27 VIII 76; Papoose Lake Turnoff (2), 27 VIII 78; Sunrise Creek, 1900 + m, 5 IX 76; Yellow Rose Mine Trail to Big Flat (2) (common), 7 IX 76; Dorleska Summit (2), 7 IX 76. (18 VII - 16 IX)

44. *Strymon melinus* Huebner. Common or Gray Hairstreak.

This widespread, weedy lowland species occurs as a rare stray in the Trinity-Eddy area, apparently much less often than in the Sierra Nevada.

HOST PLANTS: Highly polyphagous: Malvaceae, Leguminosae, *Eremocarpus*, etc.; no breeding known locally.

RECORDS: Lone Jack, 28 V 77; Deadfall Lakes, 16 IX 78; Douglas City, 2 X 76.

45. *Satyrium californica* Edwards. California Hairstreak.

This species is recorded in five localities. Two are subalpine and are among the highest records in the state. The specimens are large, very dark, and heavily marked and were taken on the host and at yellow composites, including *Haplopappus bloomeri* and *Solidago multiradiata*. They resemble Great Basin and Sierran east-slope specimens, while lower-elevation Trinity examples are more "normal" Californian. This situation deserves further study.

HOST PLANTS: Rhamnaceae: Oviposition observed on Tobacco Brush, *Ceanothus velutinus* Dougl. ex Hook., Packer's Peak.

RECORDS: Foothill: Coffee Creek, 850 m, 14 VI 80; Crawford Creek, 15 VI 80. Subalpine: S slope Russian Peak (7), 15 VI 80; Packer's Peak (6), 15 VIII 77; Deadfall Lakes, 16 VIII 79.

46. *Satyrium sylvinus* Boisduval. Sylvan Hairstreak.

Recorded from the foothills into the montane zone (fairly typical phenotypes), and (much later in the season) in boggy high-montane and subalpine boggy meadows with willow (very dark, the ventral spots more distinctly ocellate). Apparently always rare in the study area. Similar altitudinal populations occur in the northern Sierra Nevada.

HOST PLANTS: Willows (*Salix*) strongly suspected.

RECORDS: *Foothill:* Lone Jack (2), 28 V 77; Coffee Creek, 1400 m, 7 VII 77; Hobo Gulch (2), 18 VII 77. *Montane/Subalpine*: Emerald Lake, 5 VIII 79; Stuart Fork below Sawtooth Ridge (2), 5 VIII 79; Deadfall Lakes, 6 VIII 78, 16 VIII 79, (8) 16 IX 78; Packer's Peak Trail (4), 15 VIII 77; Sunrise Creek, 5 IX 76. (28 V - 18 VII; 5 VIII - 16 IX)

47. *Satyrium saepium* Boisduval. Hedgerow Hairstreak.

Locally common in foothill chaparral - mostly on serpentine - and again in montane chaparral, as at Big Flat. As with the preceding species, there is great variation in flight season with altitude and exposure, but here the phenotype is invariant. An avid flower visitor, especially to *Ceanothus, Eriogonum* spp., *Haplopappus bloomeri*, and *Chrysothamnus*.

HOST PLANTS: Undetermined locally; *Ceanothus* spp. likely.

RECORDS: lower Coffee Creek canyon, 750 m, 14 VI 80; Crawford Creek, 15 VI 80; 11 km E Callahan, 15 VI 80; Callahan, 15 VI 80; 6.5 km W Callahan, 15 VI 80; Coffee Creek, 1400 m, 7 VII 77; Morgan Meadows (4), 12 VII 79; Emerald Lake, 5 VIII 79; Carrville, 7 VIII 76; Packer's Peak trail (4), 15 VIII 77; Sunrise Creek, 5 IX 76; Parker Creek trail (7), 6 IX 76; Big Flat, 8 IX 76; Deadfall Lakes (5), 16 IX 78, 20 IX 79; Gazelle, 25 IX 77. (14 VI - 25 IX)

(47A. *Satyrium tetra* Edwards. Gray Hairstreak.

Occurs on the north slope of Mount Shasta (Military Pass Road area, near Hwy. 97), associated with Mountain Mahogany, *Cerocarpus ledifolius* Nutt., in arid montane - subalpine chaparral. This plant is abundant on Packer's Peak, above Deadfall Lakes and the south arm of Mount Eddy; the butterfly has been searched for carefully but not found. One male at a yellow composite on Russian Peak, 15 VI 80.)

(47B. *Satyrium behrii* Edwards. Behr's Hairstreak.

Has not been found in the Trinity-Eddy region despite assiduous search. Its host plant, *Purshia tridentata* (Pursh.) DC., occurs in a matted subalpine form at Packer's Peak and Dorleska Summit; it has not been seen on Mount Eddy. In the Sierra Nevada *S. behrii* does not occur in the subalpine zone either, except as a rare casual.)

48. *Satyrium fuliginosum* Edwards. Dusky Gossamer - Wing.

Trinity Alps specimens can be assigned to an undescribed subspecies which differs from Sierran material in the following characteristics: forewing broader, higher angled, especially in females; large, females often much larger than any Sierran ones; ventral forewing apex and hindwing of fresh specimens overscaled with white scales, giving a frosted or even ice-green effect; remainder of ventral forewing intensely black, especially in males; spot-pattern weak, less developed than in the Sierra Nevada. Mount Eddy and Gumboot Lake (Trinity Divide) specimens are less distinctive and seem intermediate to Sierran ones.

Our populations are virtually restricted to the subalpine zone, mostly on ultrabasics; ranging above tree line on Mount Eddy. Males perch on shrubs, especially *Quercus vacciniifolia* and *Cercocarpus ledifolius*, on rocky summits; their aerial chases are swift and spectacular, often poised in the air over sheer cliffs of 100 m or more. Both sexes visit flowers of *Eriogonum, Monardella,* and *Chrysothamnus*; females fly but little.

HOST PLANTS: *Lupinus croceus* Eastw. (Sunrise Pass, Sunrise Creek, Red Rock Mountain, Dorleska Summit, Gumboot Butte, Deadfall Lakes, Mount Eddy). Eggs are laid either on the plants or in litter around the plants; oviposition occurs infrequently amid much walking up and down the plants, on bare ground, etc. *L. croceus* is strictly endemic to ultrabasics in the Trinities and Mount Eddy. Emmel and Shields reported finding *S. fuliginosum* on granite (Sawtooth Ridge) in 1968 and saw ovipositions on *Lupinus albicaulis* Dougl. ex Hook. there and at Brown's Meadow. We have not found the insect at either location. *L. albicaulis* is the commonest lupine in montane coniferous forest in the region, mostly on non-ultrabasic soils, and its distribution correlates very poorly with that of *S. fuliginosum*.

RECORDS: Gibson Meadows (3), 30 VII 76; Granite Lake (4) 30 VII 76, (12) 31 VII 76 (apparently on the ultrabasic side of a geologically divided basin); between Granite Lake and Deer Creek, 31 VII 76; Deadfall Lakes, 6 VIII 78, (6) 16 VIII 79, (3) 27 VIII 79, 20 IX 79; Mount Eddy (6), 6 VIII 78; Gumboot Butte and Lake (3), 11 VIII 76; Sunrise Pass - Red Rock Mountain, common, 5 IX 76; above Dead Mule Camp, 5 IX 76; Dorleska Summit, 7 IX 76. (30 VII - 20 IX)

NOTE: The Trinity phenotype was figured in color by Comstock (1927), pl. 50, figs. 26 and 28. Compare to fig. 27, from Placer County.

49. *Mitoura spinetorum* Hewitson. Thicket Hairstreak.

This is the only species recorded in the Trinity Alps which we did not find in our survey. Emmel and Shields record "several at mud along the trail" at Brown's Meadow, 20 VII 68. This is a very sporadic, unpredictable species in northern California. Brown's Meadow does not seem a particularly good-looking place for it; we have sought it without success on *Chrysothamnus* at Mount Eddy, in Scott Valley, and on the north slope of Mount Shasta.

50. *Mitoura nelsoni* Boisduval. Nelson's Hairstreak.

Very abundant from the foothills to 1500 m, mostly at edges of meadows within montane coniferous forest, along trails, or in clearings where young Incense Cedars are invading sunlit areas. Adults swarm over flowering Pussy Paws and also visit *Ceanothus* and *Eriophyllum* (Compositae). There is considerable minor variation, but absolutely no tendency toward a *muiri* phenotype. Trinity - Eddy specimens are phenotypically and ecologically indistinguishable from Sierran west-slope ones.

HOST PLANTS: Cupressaceae: *Calocedrus decurrens* (Tour.) Flor.

RECORDS: Canyon Creek (3), 28 V 77; lower Coffee Creek (4), 14 VI 80; Crawford Creek, 15 VI 80; Deadfall Meadow, 15 VI 80; 11 km E Callahan (2), 15 VI 80; 6.5 km W Callahan, 15 VI 80; Deer Creek trail, 16 VI 76; Boulder Creek trail, 12 VI 76; Morris Meadow (4), 17 VI 76, (10) 24 VI 76; Willow Creek, 16 VI 76; Bridge Camp, 18 VI 76; Stuart Fork below Sawtooth Ridge, 24 VI 76; Mumford Meadow (4), 25 VI 77; Yellow Rose Mine Trail (3), 10 VII 77; Morgan Meadows (2), 12 VII 79. (28 V - 12 VII)

51. *Incisalia eryphon* Boisduval. Western Pine Elfin.

Frequent in montane coniferous forest, generally as male singletons perching on small trees in sunlit glades or at the edges of streams. It may be very common at yellow composites along the road from Cecilville to Callahan to Gazelle. There are no phenotypic differences from Sierran material.

HOST PLANTS: Presumably Pinaceae.

RECORDS: Coffee Creek, 27 V 77, (2) 14 VI 80; Shadow Creek, 29 V 77; Cecilville, 29 V 77; Deadfall Meadow, 15 VI 80; 11 km E Callahan (6) 15 VI 80; 6.5 km W Callahan, 15 VI 80; Crawford Creek, 15 VI 80; Deer Creek, 15 VI 76, 27 VI 76; Grizzly Meadows, 19 VII 77. (27 V - 19 VII)

52. *Incisalia iroides* Boisduval. Western Brown Elfin.

Not very common, mostly in montane chaparral, near *Quercus vacciniifolia*. Phenotypically indistinguishable from Sierran material.

HOST PLANTS: Unknown locally. A polyphagous species, recorded elsewhere on *Ceanothus*, Ericaceae, *Chlorogalum*, *Cuscuta*, etc.

RECORDS: Lone Jack, 28 V 77; Foster's Cabin, 13 VI 76; Coffee Creek, 800 m, 14

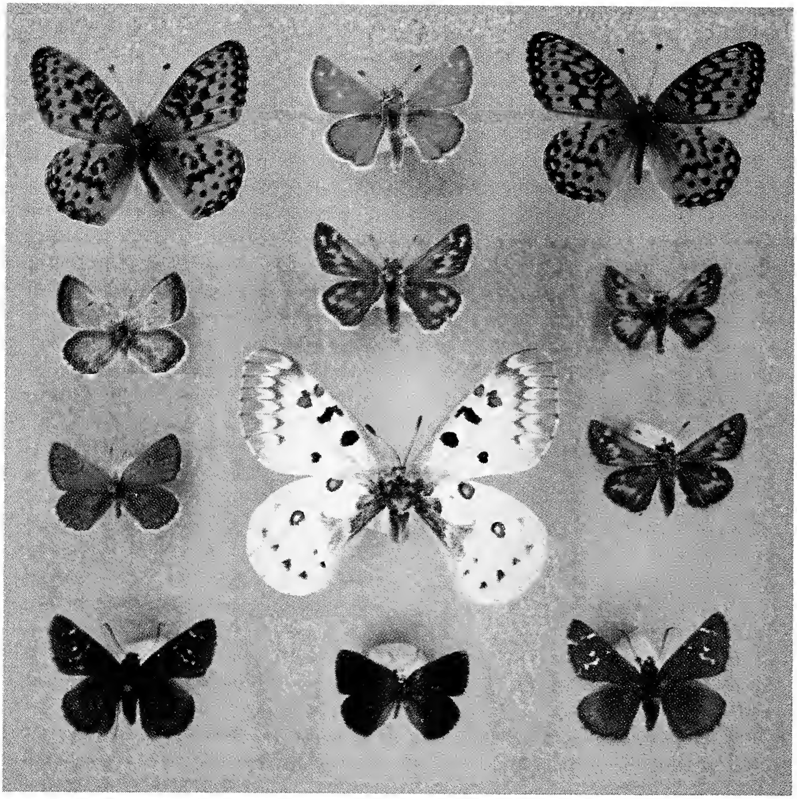

Fig. 1. Some Trinity-Eddy rarities or endemics, upper surfaces. *Speyeria mormonia erinna*: male, 16 IX 78, female, 27 VIII 79, both Deadfall Lakes; light *Hesperia harpalus*, N slope Mt. Shasta, 15 VIII 79; dark *H. harpalus*, Callahan, 21 IX 79; *Parnassius phoebus sternitzkyi*, Mt. Eddy summit, 6 VIII 78; *Agriades glandon*, Mt. Eddy, 6 VIII 78 (2); *Polites sabuleti*, Deadfal Lakes, 29 IX 79 (2); *Thorybes mexicana aemilia*, Mt. Eddy, 6 VIII 78 (2); *Satyrium fuliginosum* male, Gibson Meadows, 30 VII 76.

VI 80; Crawford Creek, 15 VI 80; 11 km E Callahan (3), 15 VI 80; 6.5 km W Callahan (3) 15 VI 80; Swift Creek, 25 VI 77; Coffee Creek, 1400 m, 26 VI 77; Mount Eddy summit, 6 VIII 78. (28 V - 6 VIII)

(52A. *Incisalia fotis windi* Clench. Wind's Hairstreak.

Not yet recorded in the study area, though it is known to occur in Trinity County. Eggs and larvae are more often collected than adults; we have searched two prospective hosts, *Sedum spathulifolium* Hook. in foothill canyons and *S. obtusatum* Gray (ssp. *boreale* Clausen) in the subalpine zone, in numerous locations without success.)

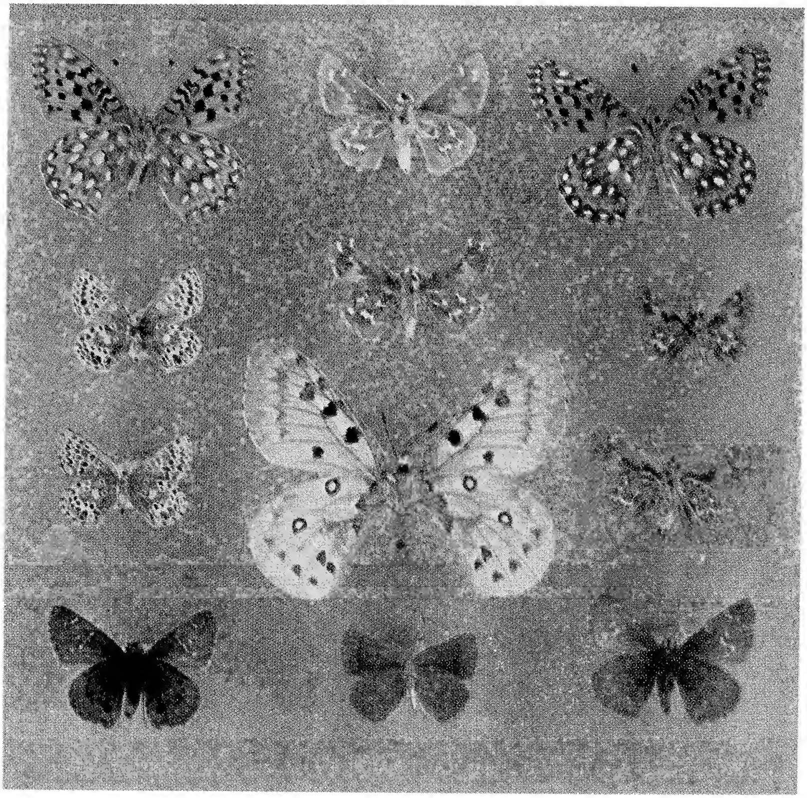

Fig. 2. Same as Fig. 1, under surfaces.

53. *Callophrys dumetorum* Boisduval. Bramble Hairstreak.

We have only one record, a worn female taken from *Vicia* flowers, and are unable to say if this is ssp. *oregonensis* Gorelick.

HOST PLANTS: Reported elsewhere on *Lotus* and *Eriogonum*.

RECORDS: Cecilville, 29 V 77.

54. *Callophrys lemberti* Tilden. Lembert's Hairstreak.

Frequent in subalpine and alpine "rock gardens," emerging immediately after snowmelt. Associated with the subalpine Trinity *Euphydryas*.

Adults visit flowering *Eriogonum* as well as small Composites. Females are redder above than Sierran *lemberti*. According to Gorelick, the northwest California populations deserve further taxonomic study.

HOST PLANTS: None confirmed. A female was collected on a budding (not flowering) *Eriogonum compositum* Dougl. ex Benth. above Sapphire Lake, but oviposition was not observed and no egg was found.

RECORDS: Lion Lake Trail, 13 VI 76; Sapphire Lake (2) 25 VI 76; Packer's Peak (2), 9 VII 77; Sunrise Pass, 10 VII 77. Recorded by S.O.M. on ridgetop NE of

Crawford Creek, and on Mount Eddy. (13 VI - 10 VII)

55. *Euphilotes battoides intermedia* Barnes and McDunnough. Square-Spotted Blue.

Frequent. Males are usually taken on mud puddles along trails and at edges of streams. Both sexes can be found around *Eriogonum umbellatum*, flying with *Plebeius lupini*, before either *Apodemia mormo* or *Lycaena heteronea* appears. Populations are known from the foothills to tree line.

HOST PLANTS: Either *Eriogonum marifolium* Torr. & Gray or *E. umbellatum* (both present).

RECORDS: Scott Valley, 29 V 77; Coffee Creek, 1400 m, 26 VI 77; Packer's Peak trail, 9 VII 77; Deadfall Lakes, 12 VII 79, 6 VIII 78; Grizzly Meadows, 10 VII 77; Gibson Meadows, 30 VII 76; Granite Lake (2), 31 VII 76; Mount Eddy (2), 6 VIII 78; Packer's Peak Summit, 15 VIII 77. (29 V - 15 VIII)

56. *Euphilotes enoptes enoptes* Boisduval. Dotted Blue.

Frequent but less widespread than the preceding, from which it is not displaced seasonally here or in the northern Sierra. The two have been found together only at Deadfall Lakes, and seem to be associated with different *Eriogonums*. Our records are from the foothills to 1150 m.

HOST PLANTS: At Lone Jack closely associated with *Eriogonum nudum* ssp. *sulphureum* (Greene) Stokes. Near Deadfall Meadow, on a white-flowered member of the same complex.

RECORDS: Lone Jack (4), 28 V 77, (3) 18 VI 77; Cecilville (2), 29 V 77; lower Coffee Creek, 14 VI 80; 6.5 km W Callahan, 15 VI 80; Callahan (3) 15 VI 80; Morris Meadow, 17 VI 76; Coffee Creek, 1400 m, 26 VI 77; Deadfall Meadow to Deadfall Lakes (2), 6 VIII 78. (28 V - 6 VIII)

57. *Glaucopsyche piasus* Boisduval. Arrowhead Blue.

One of the rarest Trinity butterflies. We have three singletons and know nothing of its ecology except that all are males taken in flowery roadside banks in the montane coniferous forest zone. The two Coffee Creek specimens were taken in the same, exact spot - 3 years apart.

In 1980 two more localities were added: Yellow Rose Mine Trail (1 ♂) and just below Sunrise Pass (2 ♀), all 27 VII 80. The two Sunrise Pass animals (2100 m) are smaller and darker than lower-elevation ones. They were very fresh.

HOST PLANTS: Unknown; *Lupinus* elsewhere.

RECORDS: Coffee Creek, 850 m, 27 V 77, 14 VI 80; Lion Lake trail, 13 VI 76.

58. *Glaucopsyche lygdamus incognitus* Tilden. Silvery Blue.

Common in lower Coffee Creek Canyon. Otherwise generally scarce, occurring mostly in moist, grassy situations where tall lupines grow; found once above tree line. In the Red Trinities it often occurs on the *Darlingtonia* bogs.

Variation in this species is complex. Our low-elevation series is fairly typical *incognitus*. High-elevation specimens resemble *columbia* Skinner, while our only Scott Valley specimen, a female, is strikingly different from both - fawn-gray beneath, with very large black spots. The Trinity-Eddy area may thus be one of rapid subspecific transition.

HOST PLANTS: Leguminosae: *Lupinus latifolius* Agardh. strongly suspected on the bogs. In lower Coffee Creek Canyon associated with weedy (introduced) *Vicia* spp. and the native *Lathyrus jepsonii* ssp. *californicus* (Wats.) Hitchc. Host on Mount Eddy unknown.

RECORDS: Coffee Creek, to 1000 m (25), 27 V 77; Canyon Creek (2), 28 V 77; Scott Valey, 29 V 77; Lone Jack, 28 V 77; Lion Lake Trail, 13 VI 76; Bear Basin, 15 VI 76; Deadfall Meadow, 15 VI 80; 6.5 km W Callahan, 15 VI 80; Willow Creek (2), 16 VI 76; Morris Meadow, 17 VI 76; Deer Creek, 27 VI 76; Mount Eddy, near summit, fresh, 6 VIII 78. (27 V - 6 VIII)

59. *Celastrina argiolus echo* Edwards. Echo Blue.

The commonest Blue in the Trinity-Eddy region, ranging from the foothills to subalpine habitats, but commonest in montane coniferous forest. It is the first non-hibernator to appear in spring; on 27 V 77 a fresh male was taken flying over continuous snow cover at the LeRoy Mine. Variation in our series is minimal, and there is no trace of a second brood.

HOST PLANTS: Undetermined; *Ceanothus* spp. suspected.

RECORDS: Yellow Rose Mine Trail, 27 V 77; Lone Jack (4), 28 V 77; Crawford Creek (4), 29 V 77; Cecilville, 29 V 77; Boulder Creek (6), 12 VI 76; Lion Lake Trail, 13 VI 76; Union Creek (2) 14 VI 76; lower Coffee Creek, 14 VI 80; Eagle Creek, 14 VI 80; Deadfall Meadow, 15 VI 80; 3.2 km W Gazelle, 15 VI 80; 6.5 km W Callahan, 15 VI 80; Deer Creek (3), 16 VI 76, 27 VI 76; Willow Creek, 16 VI 76; Morris Meadow (2), 17 VI 76, 26 VI 76; Stuart Fork below Sawtooth Ridge, 24 VI 76; Swift Creek, 25 VI 77; Emerald Lake (2) 25 VI 76; Sapphire Lake, 25 VI 76; Coffee Creek, 26 VI 77; base of Red Rock Mountain, 10 VII 77; Grizzly Meadows (2), 19 VII 77; Mount Eddy, 6 VIII 78. (27 V - 6 VIII)

60. *Lycaeides argyrognomon* Berg complex. Anna Blue, Rice's Blue.

These populations are among our most complex and confusing. Several phenotypes and ecotypes occur in the Trinity-Eddy area. Most specimens are referable to ssp. *anna* Edwards, but some from bog meadows look very like *ricei* Cross. Distinct populations occur in two very different habitats: on bogs, seeps, and wet meadows around 1500 m, and in xeric open sites near to above tree line, some 1000 m higher. On the average, bog females have less orange above than subalpine ones, but a few bog females have no orange on the forewing at all. See also the next species.

HOST PLANTS: Leguminosae. Bog populations are *always* associated with *Lotus oblongifolius* (Benth.) Greene var. *nevadensis* (Gray) Munz. Subalpine populations, including the rather lower-altitude one at Gumboot Butte, are *always* associated with *Astragalus whitneyi* var. *siskiyouensis* (Rydb.) Barneby, a plant confined to ultrabasic soils (except on Packer's Peak). On 6 VIII 78 the subalpine population at 2650 m on Mount Eddy was more advanced than the meadow one at Deadfall Lakes, 450 m lower.

RECORDS: *Bog populations:* Morris Meadow, 17 VI 76, (6) 26 VI 76, (2) 4 VIII 79; Deer Creek, 27 VI 76; Mumford Meadow, 25 VI 77; Gibson Meadows (4) 30 VII 76; Morgan Meadows (10), 12 VII 79; Grizzly Meadows (2), 18 VII 77; Deadfall Lakes (7), 6 VIII 78, 16 VIII 79, 27 VIII 79, 16 IX 78; Dead Mule Camp (9), 5 IX 76; Parker Creek Trail, 6 IX 76. (17 VI - 16 IX) *Subalpine Populations:* Packer's Peak, 9 VII 77, (4) 15 VIII 77; Mount Eddy, near summit, (2) 6 VIII 78, 16 VIII 79; Gumboot Butte, 11 VIII 76. (9 VII - 16 VIII)

61. *Lycaeides melissa* Edwards. Melissa Blue.

Melissa is abundant in Scott Valley and along the Callahan - Gazelle Road, where it is a multiple-brooded pest of cultivated Alfalfa. It has also been collected at high elevations associated with *Astragalus whitneyi*, but the populations are not phenotypically differentiated and it is not clear whether or not *melissa* is a permanent resident in the high country. The subalpine *melissa* from the Trinity-Eddy area are different from the animal associated with the same legume around Sonora and Carson Passes in the central Sierra. (This animal has been variously identified as an *argyrognomon* and a *melissa*.)

HOST PLANTS: In Scott Valley, Alfalfa (*Medicago sativa* L.). At Packer's Peak and Gumboot Butte, apparently *Astragalus whitneyi* ssp. *siskiyouensis* (Rydb.) Barneby.

RECORDS: *Multivoltine*: Scott Valley, 29 V 77, (2) 15 VI 80, (55) 21 IX 79; Callahan, 15 VI 80, (12) 16 VIII 77; 3.2 km W Gazelle (7), 5 VII 80; French Creek (Scott Valley) (2), 21 IX 79. *Univoltine*: Gumboot Butte, 11 VIII 76; Packer's Peak (2), 15 VIII 77; Deadfall Lakes (6), 20 IX 79.

62. *Plebeius saepiolus* Boisduval. Greenish Blue.

Abundant and general in meadows and bogs, from the upper foothills to near tree line. Apparently always univoltine, with red-brown females only. Trinity-Eddy specimens average larger than Sierran ones from the same elevations, and are more boldly marked beneath. Many Eddy-Deadfall females have a submarginal row of black dashes visible dorsally. The Greenish Blue often flies with the Gray Blue in bogs, and the two may be difficult to distinguish in flight. We have several times found *saepiolus* roosting head down on low plants in boggy meadows at daybreak, completely covered with frost.

HOST PLANTS: *Trifolium longipes* Nutt., *T. wormskjoldii* Lehm., and *T. productum* Greene (all from several stations).

RECORDS: Cecilville (2) 29 V 77; Mumford Meadow (2), 14 VI 76, (6) 25 VI 77; Eagle Creek, 14 VI 80; Deadfall Meadow, 15 VI 80, (28) 12 VII 79, (2) 16 VIII 79, 20 IX 79; Willow Creek, 16 VI 76; Morris Meadow (6), 17 VI 76, (3) 24 VI 76; Deer Creek (4) 27 VI 76; Coffee Creek, 26 VI 77; Gulick Creek (3) 10 VII 77; Scott Mountain Summit (2) 11 VII 77; Morgan Meadows (11), 12 VII 79; Grizzly Meadows (4), 19 VII 77; Gibson Meadows (2) 31 VII 76; Granite Lake, 31 VII 76; Mount Eddy (2), 6 VIII 78, 16 VIII 79; Deadfall Lakes (9), 6 VIII 78. (29 V - 20 IX)

63. *Plebeius icarioides* Boisduval. Icarioides Blue.

This is the commonest Blue in open montane coniferous forest; it also occurs at the edges of dry meadows, but ranges less widely than the Echo Blue and, except on Mount Eddy, rarely over 1850 m. It varies but little, averages more heavily marked beneath than Sierran *icarioides* from similar elevations, and in general resembles North Coast Range and Yolla Bolly series. We have not found any dwarfed high-altitude populations like the one on Goat Mountain in the Yolla Bollys. One brood, early - to midsummer.

HOST PLANTS: Leguminosae: *Lupinus albicaulis* Dougl. ex Hook. (Brown's Meadow, 10 VIII 76) (generally associated). Oviposited on an undetermined lupine, not in flower, on Mount Eddy. It is not known if this species uses *Lupinus croceus*, the host of *Satyrium fuliginosum*, with which it is rarely sympatric.

RECORDS: Lone Jack, 28 V 77; Mumford Meadow (2), 14 VI 76, (8) 25 VI 77; Coffee Creek (2) 14 VI 80, 26 VI 77; Eagle Creek, 14 VI 80; Crawford Creek, 15 VI 80; Morris Meadow, 17 VI 76, 24 VI 76; Bridge Camp (4) 18 VI 76; Deer Creek (2) 27

VI 76; base of Red Rock Mountain (5), 10 VII 77; Yellow Rose Mine trail (2), 10 VII 77; Deadfall Lakes, 12 VII 79, (2) 8 VIII 78; Grizzly Meadows, 18 VII 77; Mount Eddy (4), 6 VIII 78; Brown's Meadow, 10 VIII 76; Packer's Peak trail (4), 15 VIII 77. (28 V - 15 VIII)

64. *Plebeius acmon* Westwood and Hewitson. Acmon Blue.

Common and general; a weedy species of open country, capable of turning up almost anywhere, even in the remotest valleys. We doubt that it overwinters above 1000 m in this region. Multiple brooded, with some seasonal variation, but usually easy to distinguish from *P. lupini*.

HOST PLANTS: Polygonaceae: *Eriogonum nudum* ssp. *sulphureum* (Greene) Stokes (Lone Jack and Hwy. 3); *E. umbellatum* Torr. (Canyon Creek and Packer's Peak). Leguminosae: *Lotus purshianus* (Benth.) Clem. and Clem. (Big Flat); *L. denticulatus* (Drew) Greene and *L. humistratus* Greene, many stations.

RECORDS: Lone Jack, 27 V 77; Canyon Creek, 28 V 77; Scott Valley, 29 V 77; Lion Lake Trail, 13 VI 76; Mumford Meadow (2), 14 VI 76; Coffee Creek, 800 m, (4) 14 VI 80; Eagle Creek, 14 VI 80; lower Bear Basin Meadow, 15 VI 76; Morris Meadow, 14 VI 76, 17 VI 76, 26 VI 76; Crawford Creek (3), 15 VI 80; Deadfall Meadow, 15 VI 80; Callahan, 15 VI 80; 6.5 km W Callahan, 15 VI 80; Willow Creek (?), 16 VI 76; Deer Creek (2) 16 VI 76, 27 VI 76; Cold Spring (2), 24 VI 76; Emerald Lake, 25 VI 76; Coffee Creek, 1400 m, (3) 26 VI 77; 3.2 km W Gazelle (2) 5 VII 80; Packer's Peak trail, 9 VII 77; Yellow Rose Mine Trail, 10 VII 77, 5 IX 76; Sunrise Pass (4), 10 VII 77; Deadfall Lakes (4) 8 VIII 78, (3) 16 IX 78; Carrville (2), 7 VIII 76; cirque above Josephine Lake, 8 VIII 76; Brown's Meadow, 10 VIII 76; Packer's Peak, 15 VIII 77; Douglas City, 29 VIII 79; Sunrise Creek (3), 5 IX 76; Union Creek Trail (2), 6 IX 76; Deadfall Meadow (3), 20 IX 79; Big Flat, 25 IX 77. (27 V - 25 IX)

65. *Plebeius lupini* Boisduval. Lupine Blue.

This mis-named Blue is common in the vicinity of its host - Sulphur Flower, *Eriogonum umbellatum* - from the foothills to the top of Mount Eddy. Unlike *P. acmon*, it is strictly univoltine, but the flight season is very long. Trinity-Eddy specimens are subtly different from Sierran ones in various color and pattern characters.

Throughout its great altitudinal range, *lupini*, like its host plant, prefers sandy or gravelly areas including talus slopes and mine tailings. It does not seem to colonize plants in seasonal streambeds subject to inundation. It strays to meadows and is occasionally taken on mud puddles.

HOST PLANTS: *Eriogonum umbellatum* Torr. complex (many stations).

RECORDS: Coffee Creek, 850 m, 27 V 77; Canyon Creek, 28 V 77; Lone Jack (3), 28 V 77, 18 VI 77; Eagle Creek (9), 14 VI 80; Crawford Creek (2), 15 VI 80; Mumford Meadow, 25 VI 77; Emerald Lake (3), 25 VI 76; Coffee Creek, 1400 m (2), 26 VI 77; Stuart Fork below Sawtooth Ridge (2), 24 VI 76, 5 VII 79; Morris Meadow (3), 26 VI 76; Sunrise Pass, 10 VII 77; Deadfall Lakes, 12 VII 79, 6 VIII 78, 20 IX 79; Grizzly Meadows (5), 19 VII 77; Granite Lake (3), 31 VII 76; Granite Creek (2), 30 VII 76; Mount Eddy, near summit (2), 6 VIII 78, fresh male 16 IX 78; Caribou Basin, 9 VIII 76. (27 V - 20 IX)

66. *Agriades glandon* Prunner. Gray Blue.

The name of our Gray Blue has bounced around in the literature. Determinations of conspecificity with Palaearctic taxa are shaky at best, and there are probably two or three genetic species in North America. Whatever one calls it, the Gray Blue is a consistent inhabitant of *Darlingtonia* bogs in the Red Trinities and on Mount Eddy, flying with *Plebeius saepiolus, Thorybes mexicana aemilia, Chlosyne hoffmanni segregata,* and *Phyciodes campestris*. We have never found it on the small heather bogs on granite. It does occur in the Caribou Basin.

Trinity-Eddy populations are more boldly marked beneath than Sierran *podarce* Felder and Felder. They also average larger and broader-winged. Females vary from plain chestnut-brown above to conspicuously white-dotted on the disc. Similar forms occur in high-altitude *podarce*.

HOST PLANTS: Primulaceae: *Dodecatheon jeffreyi* Van Houtte (many stations).

RECORDS: Eagle Creek, 14 VI 80; Deer Creek, 16 VI 76, (9) 27 VI 76; Mumford Meadow (11), 25 VI 77; Gulick Creek (4), 10 VII 77; Scott Mountain summit (7), 11 VII 77; Morgan Meadows (2), 12 VII 79; Deadfall Lakes (4), 12 VII 79, (2) 6 VIII 78, (12) 27 VIII 79; Mount Eddy (9), 6 VIII 78, (3) 16 VIII 79; Caribou Basin (6), 9 VIII 76; upper Caribou Lakes Trail, 1850 m, 10 VIII 76; Sunrise Creek, 5 IX 76. (14 VI - 5 IX)

67. *Everes amyntula* Boisduval. Western Tailed Blue.

Like the Anna Blue, this species occurs in different habitats on different Leguminous hosts. In the foothill canyons and lower montane coniferous forest it occurs in small clearings and along stream edges, with a small vetch; at mid-elevations, in successful thickets at the edges of meadows, often with Bracken, associated with a larger vetch; and near to above tree line it swarms over the common alpine locoweed. Alpine specimens average darker and duller than others, with larger black dots beneath.

The Western Tailed Blue is univoltine everywhere in our area, except possibly for the fresh male collected 20 IX 79 at Deadfall Meadow.

HOST PLANTS: Leguminosae: *Vicia californica* Greene (Crawford Creek); *Lathyrus jepsonii* ssp. *californicus* (Wats.) Hitchc. (Deer Creek); *Astragalus whitneyi* ssp. *siskiyouensis* (Rydb.) Barneby (Packer's Peak, Mount Eddy). Larvae feed on green seeds inside pods, sealing up the entrance hole with silk.

RECORDS: Lone Jack, 28 V 77; Shadow Creek (2), 29 V 77; Crawford Creek (4), 29 V 77, (2) 15 VI 80; Canyon Creek (5), 28 V 77; Stuart Fork below Sawtooth Ridge (4), 24 VI 76; Deer Creek (6), 27 VI 76; Packer's Peak, near summit (5), 9 VII 77; Morgan Meadows, 12 VII 79; Deadfall Lakes (3), 12 VII 79, (5) 6 VIII 78, 27 VIII 79; Mount Eddy, summit area and south arm (28), 6 VIII 78; Deadfall Meadow, 20 IX 79. (28 V - 20 IX)

PIERIDAE

68. *Colias philodice eriphyle* Edwards. Yellow Sulphur.

Common in Alfalfa fields, Scott Valley and Callahan - Gazelle Road, with the Melissa Blue. This sulphur apparently strays south along Highway 3 to south of Weaverville, and breeds sporadically and unreliably in the Trinities. It cannot be considered a permanent resident there. Hybrids with *C. eurytheme* have been found at Callahan. Three broods, the late fall specimens heavily melanized below and vaguely whitish above ("*anthyale*").

HOST PLANTS: Leguminosae: Alfalfa (*Medicago sativa* L.), probably others.

RECORDS: 3.2 km W Gazelle (5), 15 VI 80, (20) 5 VII 80; Callahan (8), 16 VIII 77; French Creek (Scott Valley) (3), 21 IX 79; Gazelle, 3 IX 77; Parker Meadow, fresh male, 1 X 76; Douglas City, female, 2 X 76. Hybrids: 3.2 km W Gazelle (4), 5 VII 80; Callahan (2), 16 VIII 77. (15 VI - 2 X)

69. *Colias eurytheme* Boisduval. Orange Sulphur.

Common everywhere, from the foothills to above tree line. Females run 40-50% white. We suspect that *C. eurytheme* does not overwinter above 1000 m in the Trinity-Eddy area, since all the high-elevation records for June are of second-generation phenotypes which could not be from overwintered larvae. We also doubt that it overwinters reliably in Scott Valley. One *semialba* female, Union Creek, 6 IX 76.

HOST PLANTS: Leguminosae: *Trifolium longipes* Nutt., *wormskjoldii* Lehm., *pratense* L., all oviposition records at Morris Meadow, VI 1976; *Medicago sativa* L., Scott Valley; probably others.

RECORDS: Coffee Creek, 850 m, 27 V 77, 14 VI 80; Lone Jack, 28 V 77; Lion Lake trail, 13 VI 76; Parker Meadow (3), 14 VI 76; Eagle Creek (2), 14 VI 80; Mumford Meadow (2), 14 VI 76, (4) 25 VI 77; ridge between Bear and Black Basins (2), 15 VI 76; Crawford Creek, 15 VI 80; Deadfall Meadow, 15 VI 80; road 42N17, 1.1 km N Deadfall Meadow, 15 VI 80; 11 km E Callahan, 15 VI 80; Willow Creek (3), 16 VI 76; Morris Meadow (3), 17 VI 76, 24 VI 76, 26 VI 76; Union Creek (2), 14 VI 76, (4) 6 IX 76; Coffee Creek, 1400 m, 26 VI 77; 3.2 km W Gazelle (6), 5 VII 80; Packer's Peak, 9 VII 77; base of Red Rock Mountain (5), 10 VII 77; Morgan Meadows, 12 VII 79; Deadfall Lakes, 12 VII 79, 6 VIII 78, 16 VIII 79, (8) 16 IX 73, 20 IX 79; Grizzly Meadows, 19 VII 77; Granite Creek, 30 VII 76; Granite Lake, 31 VII 76; Mount Eddy, 6 VIII 78; Yellow Rose Mine Trail, 5 IX 76; Dead Mule Camp (3), 5 IX 76; French Creek (Scott Valley) (3) 21 IX 79; Big Flat, 24 IX 77; Swift Creek, 1 X 76; Douglas City, 2 X 76. (27 V - 2 X)

70. *Colias occidentalis chrysomelas* H. Edwards. Golden Sulphur.

Our only Sulphur of the forest; never seen in meadows. Frequent in lower montane coniferous forest among Yellow Pine and Douglas Fir, often occurring with *Anthocharis lanceolata, Pieris napi, Carterocephalus palaemon,* and *Plebeius icarioides*. No truly white females have been collected, but we have a "whitish" one from Hobo Gulch. One brood.

HOST PLANTS: Leguminosae: Associated with *Lupinus albicaulis* Dougl. ex Hook. and *Lathyrus pauciflorus* Fern. ssp. *browni* (Eastw.) Piper.

RECORDS: Lone Jack (4), 18 VI 77; Hobo Gulch (6), 18 VII 77; Crawford Creek (S.O.M.). (18 VI - 18 VII)

71. *Neophasia menapia* Felder and Felder. Pine White.

The Pine White is abundant from the foothill canyons to above 6000 feet, usually in clearings, along trails, or at the edges of meadows within montane coniferous forest. Deep in the forest, individuals may be seen 30 or 40 feet off the ground. Visits *Aster, Chrysothamnus,* and *Haplopappus bloomeri* freely.

Trinity-Eddy specimens are rarely heavily enough marked to match the description of Coast Range *tau* Scudder; most would fit within the variational range of Sierran material.

At 900 m this species flies in late June and July, while at 1500 m it is not seen until early September and then flies into October. This is *not* a steady progression in emergence dates as one moves upslope; there seems to be a sharp phenological discontinuity. The same phenomenon occurs between 1500 and 2100 m in Nevada County, on the Sierran west slope. Emmel and Shields recorded the

Pine White at 1900 m, high on the Caribou Lakes Trail, 20 VII 68. We have never seen it at this elevation until a full month or more later. It was not present on this trail on 10 VIII 76 and was not seen 400 m lower at Big Flat for almost a month.

HOST PLANTS: Not determined here; presumably Pinaceae.

RECORDS: Trinity Summit, 1100 m (3), 9 VII 77; Hobo Gulch (4), 18 VII 77; Deer Creek, 5 VIII 79; Packer's Peak Trail, 1750 m, 15 VIII 77; Papoose Lake turnoff, 27 VIII 76; Bob's Farm, 27 VIII 76; Sunrise Creek, 5 IX 76; Big Flat (5), 7 IX 76, (3) 8 IX 76,(6) 30 IX 76; Yellow Rose Mine Trail (5), 7 IX 76; below Deadfall Meadow, 16 IX 78; Swift Creek (13), 1 X 76. (9 VII - 1 X)

(71A. *Pieris beckerii* Edwards. Becker's White.

Not recorded in the Trinities or on Mount Eddy, but apparently resident in Scott Valley and as far west as Callahan; therefore to be expected as a stray.

HOST PLANTS: Undetermined locally.

RECORDS: 3.2 km W Gazelle (2), 15 VI 80; Callahan, 16 VIII 77; Scott Valley, 21 IX 79.)

72. *Pieris sisymbrii* Boisduval. California White.

This is a common species in the high country of both the granite and ultrabasic Trinities. It has been recorded hilltopping on ridges and summits from 1800 to 2700+ m. Females occasionally turn up in creek bottoms at lower elevations. Mount Eddy material averages larger than Trinity. All specimens are very heavily marked; females run 50% white, 50% yellow. Strictly univoltine.

HOST PLANTS: Undetermined in the Trinities; probably *Streptanthus, Arabis,* or *Draba* species, never found with weedy, introduced Crucifers. On Mount Eddy on the endemic semi-succulent Crucifer *Streptanthus barbatus* Wats.

RECORDS: Lion Lake Trail, 13 VI 76; between Lion Lake and Foster Lake, 13 VI 76; ridge between Bear and Black Basins (3), 15 VI 76; road 42N17, 1.1 km N Deadfall Meadow, flying over snow, 15 VI 80; Coffee Creek, 1400 m, 26 VI 77; Deer Creek, 27 VI 76; Deadfall Lakes (4), 12 VII 79; Mount Eddy summit (3), 6 VIII 78. (13 VI - 6 VIII)

73. *Pieris protodice* Boisduval and LeConte. Checkered White.

Probably not a regular resident. This lowland species had a "boom" year in 1977 and spread very widely in northern California, but subsequently disappeared from almost all of this extended range. It was not found in the study area in 1976, 1978 or 1979. Its nearest "permanent" populations are at the head of the Central Valley at Turtle Bay, Redding.

HOST PLANTS: Oviposition seen on *Rorippa curvisiliqua* (Hook.) Bessey in a dry stream bed, Mumford Meadow, 25VI 77.

RECORDS: Mumford Meadow (5), 25 VI 77; Coffee Creek, 1400 m, 26 VI 77; Hwy. 3 at Swift Creek (8), 10 VII 77; Packer's Peak (9), 15 VIII 77; Big Flat, 25 IX 77. (25 VI - 25 IX)

74. *Pieris occidentalis* Reakirt. Western White.

The Western White is the only butterfly that rivals the Western Tailed Blue in abundance at 2700 m. It occurs from 1500 m to the highest summits, but breeds at 850 m on the floor of Scott Valley where *P. protodice* seems not to occur. There is tremendous individual variation. A few extreme *calyce* Edwards have been taken, mostly on Mount Eddy. This is a phenotype induced by short days and pupal chilling after diapause. Of about 203 specimens, only 27 are females; this reflects the hilltopping behavior of the males, rendering them much easier to find.

It is not unusual to find 3 or 4 species of white Pierids, plus *Parnassius phoebus sternitzkyi*, hilltopping on the same summit; usually at least 75% of the specimens will be *P. occidentalis*. At least partially double-brooded; perhaps partially triple-brooded in Scott Valley.

HOST PLANTS: Ovipositions have been seen on the following Crucifers: *Descurainia richardsonii* ssp. *viscosa* (Rydb.) Detl.; *Draba howellii* Wats.; *D. crassifolia* Grah.; *Athysanus pusillus* (Hook.) Greene; *Arabis platysperma* Gray; *A. breweri* Wats.; *Lepidium campestre* (L.) R.Br.; *Pheonicaulis cheiranthoides* Nutt. in T. & G.; *Streptanthus tortuosus* Kell.; *S. barbatus* Wats. Probably others will be found.

RECORDS: 11 km E Callahan, 15 VI 80; 6.5 km W Callahan, 15 VI 80; 3.2 km W Gazelle (2), 15 VI 80; Callahan, 15 VI 80; Packer's Peak (4), 9 VII 77, (39) 15 VIII 77, 30 IX 76; Sunrise Pass and Red Rock Mountain (20), 10 VII 77, (8) 5 IX 76; Deadfall Lakes (6), 12 VII 79, (3) 16 VIII 79, (7) 16 IX 78; Grizzly Meadows, 19 VII 77; Mount Eddy, mostly near summit (93), 6 VIII 78, (10) 16 IX 78; Parker Creek divide (8), 6 IX 76; Dead Mule Camp (7), 5 IX 76; Dorleska Summit (2), 7 IX 76; Callahan (3), 21 IX 79; French Creek (Scott Valley) (3), 21 IX 79; Big Flat, 25 IX 77. (15 VI - 30 IX)

75. *Pieris napi* Linnaeus. Gray-Veined White.

Frequent in montane coniferous forest, mostly below 2100 m. Occurs mainly in moist canyon bottoms. Trinity *napi* are smaller and more lightly marked than typical *microstriata* Comstock, showing some resemblance to *marginalis* Scudder of western Oregon, and also to the unnamed Warner Mountains population which, however, is multivoltine and lives in boggy meadows. These are strictly univoltine and monophenic in the wild, but we have reared a brood of 16 nearly immaculate second-brood specimens from laboratory, non-diapause pupae (eclosed late VI - early VIII, 1977; Shadow Creek stock on *Brassica campestris* L.).

No *napi* have been recorded from Mount Eddy.

Often found flying with *Anthocharis lanceolata*, only infrequently at flowers. Difficult to collect because males, in particular, fly 20 feet or more off the ground.

HOST PLANTS: The following Crucifers are common in *napi* habitats. No definite hosts have been recorded: *Dentaria californica* Nutt. and var. *cardiophylla* (Greene) Detl.; *Cardamine breweri* Wats.; *C. lyallii* Wats.; *Thlaspi glaucum* Nels. var. *hesperium* Pays.

RECORDS: Canyon Creek (2), 28 V 77; Cecilville (2), 29 V 77; Crawford Creek (5), 29 V 77; Shadow Creek, 29 V 77; Parker Meadow, 14 VI 76; Coffee Creek, 800 m (2), 14 VI 80; 11 km E Callahan, 15 VI 80; Callahan, 15 VI 80; Deer Creek, 15 VI 76, 16 VI 76, (2) 27 VI 76; Willow Creek, 16 VI 76; Lone Jack, 18 VI 77; Stuart Fork below Sawtooth Ridge, 25 VI 76; Coffee Creek, 1400 m, 26 VI 77. (28 V - 27 VI)

76. *Pieris rapae* Linnaeus. European Cabbage Butterfly.

Occasional. Not very common, perhaps resident only at lower levels. It definitely overwinters in Scott Valley and at Cecilville, but June-July specimens at higher elevations are second-brood flyups from the Central Valley (?). Meadows, and along trails and streams.

HOST PLANTS: Not recorded in the Trinities; presumably Cruciferae.

RECORDS: Scott Valley, 29 V 77, 21 IX 79; Crawford Creek, 29 V 77; Shadow Creek, 29 V 77; Cecilville, 29 V 77; Coffee Creek, 800 m, 14 VI 80; Callahan, 15 VI

80; Morris Meadow, 24 VI 76; Coffee Creek, 1400 m, (2) 26 VI 77; Swift Creek, 25 VI 77; Packer's Peak trail, 9 VII 77, (2) 15 VIII 77; Deadfall Lakes (2), 6 VIII 78, (2) 16 IX 78; Big Flat, 7 IX 76; French Creek (Scott Valley), 21 IX 79; Etna, 21 IX 79. (29 V - 21 IX)

77. *Anthocharis sara* Lucas. Sara Orange - Tip.

Infrequent, recorded in foothill and lower montane canyons in the Trinities, thus far not on Mount Eddy; almost all jour specimens are males, and all are white. There is no trace of yellow ground-color characteristic of high-elevation and east-slope Sierran populations, and the white *sara* do not expand into their niche. Single-brooded.

HOST PLANTS: Undetermined, presumably Crucifers.

RECORDS: Coffee Creek, 850 m (4), 27 V 77; Canyon Creek, 28 V 77; Lone Jack, 28 V 77; Crawford Creek, 29 V 77; Scott Valley, 29 V 77; Shadow Creek, 29 V 77; 6 km W Callahan, 15 VI 80; Deer Creek, 27 VI 76. (27 V - 27 VI)

78. *Anthocharis lanceolata* Lucas. Boisduval's Marble.

Usually a scarce butterfly, Boisduval's Marble is common everywhere in the Trinities that *Pieris napi* occurs, and ranges higher in the same canyons. Like that species, it is not yet recorded from Mount Eddy. Our specimens vary in size but average smaller than Sierran ones; there seem to be no phenotypic distinctions among Coast Range, Trinity, and Sierra *lanceolata*. The butterfly rarely visits flowers, and is difficult to catch.

HOST PLANTS: Ovipositions as follows: *Arabis holboellii* Horn. var. *retrofracta* (Grah.) Rydb. (Deer Creek, 27 VI 76); *A. glabra* (L.) Bernh. (Lone Jack, 28 V 77). Probaly other Crucifers as well.

RECORDS: Lone Jack, 28 V 77; Canyon Creek (2), 28 V 77; Soctt Valley, 29 V 77; Cecilville (3), 29 V 77; Coffee Creek, 800 m, 14 VI 80; 6.5 km W Callahan (4), 15 VI 80; Deer Creek (4), 27 VI 76; Coffee Creek, 1400 m, 7 VII 77; Packer's Peak Trail, 9 VII 77. (28 V - 9 VII)

79. *Euchloe ausonides* Lucas. Large Marble.

Here again, there are high- and mid-altitude populations differing in ecology and phenotype. Above 1500 m occurs the small, Sierran - type "alpine *ausonides*" - a hilltopper usually found coursing over bare rock at or near summits. In lower habitats occurs a larger *ausonides* similar to that found in the Central Valley. Near Gazelle this animal is double-brooded. The entire complex requires further study.

HOST PLANTS: *Descurainia* sp. (Deadfall Lakes, a dead specimen damaged in *ausonides* fashion, 16 VIII 79; one larva, 3.2 km W Gazelle, 5 VII 80); *Lepidium* sp. (Scott Valley, 14 VI 80). Probably a variety of Crucifers.

RECORDS: Coffee Creek, 850 m (7), 27 V 77; 11 km E Callahan, 15 VI 80; Callahan, 15 VI 80; 6.5 km W Callahan (3), 15 VI 80; Mumford Meadow, 25 VI 77; Deadfall Lakes, 12 VII 79; Grizzly Meadows, 19 VII 77; Caribou Basin, 21-22 VII 68 (Emmel and Shields, not found by us). Second brood: 3.2 km W Gazelle (6), 5 VII 80. (27 V - 22 VII)

80. *Euchloe hyantis* Edwards. Edwards' Marble.

Commoner and more general than the preceding; foothills to above tree line, but usually found hilltopping on high, bleak ridges with *Pieris occidentalis* and *P. sisymbrii*. Males also patrol vertical rock faces at canyon bottoms. There are no phenotypic differences from Sierran specimens, and the large, bright phenotype found in foothill canyons in the Coast Ranges has not been observed in our area.

HOST PLANTS: Probably among *Streptanthus, Arabis,* and *Draba* (Cruciferae).

RECORDS: Coffee Creek, 850 m, (4), 27 V 77; Lone Jack, 28 V 77; Scott Valley, 29 V 77; ridge above Deer Creek, 15 VI 76; 6.5 km W Callahan (3), 15 VI 80; Sapphire Lake (2), 25 VI 76; Mumford Meadow, 25 VI 77; Morris Meadow, 26 VI 76; Packer's Peak, 9 VII 77; Deadfall Lakes, 12 VII 79; Mount Eddy summit (4), 6 VIII 78. (27 V - 6 VIII)

PAPILIONIDAE

81. *Papilio zelicaon* Lucas. Anise Swallowtail.

Very common and widespread from the foothills to the alpine zone, mostly seen as a hilltopper. Probably partially double-brooded, at least at low elevations. The interpretation of the long flight season is confounded by vertical movements. There is considerable individual variation; a few specimens have an orange flush below, and the Emerald Lake female has it above as well. Visits *Monardella* and other butterfly flowers.

HOST PLANTS: Umbelliferae: *Angelica arguta* Nutt. ex T. & G. (numerous stations, eggs and larvae; the commonest large Umbellifer in the Trinities).

RECORDS: Coffee Creek (5), 27 V 77, 26 VI 77; Scorpion Creek, 28 V 77; Parker Meadow, 14 VI 76; Union Creek, 14 VI 76; Scott Valley (2), 15 VI 80; 11 km E Callahan, 15 VI 80; Emerald Lake (2), 25 VI 76; Mumford Meadow, 25 VI 77; 3.2 km W Gazelle, 5 VII 80; Sunrise Pass (9), 10 VII 77, 5 IX 76; base of Red Rock Mountain, 10 VII 77; Deadfall Lakes, 12 VII 79, 16 IX 78; Grizzly Meadows, 19 VII 77; Mount Eddy summit area (26), 6 VIII 78, (2) 16 IX 78; Packer's Peak summit (7), 15 VIII 77. (27 V - 16 IX)

82. *Papilio indra* Reakirt. Indra Swallowtail.

Occasional over a wide elevational range, but never common anywhere. We have six specimens - four from mud puddles and two hilltopping. When *P. indra* "hilltops" it typically flies just *below* the crest, rarely mixing with *P. zelicaon* at the top. This habit makes it easy to overlook, and difficult to catch even if seen. Phenotypically these are like northern Sierran *indra,* not like the phenotype that occurs on serpentine in the North Coast Range.

HOST PLANTS: Undetermined; probably Umbelliferae.

RECORDS: Lone Jack, 28 V 77; Crawford Creek, 15 VI 80; Morris Meadow (2), 26 VI 76; Mount Eddy, summit area (2), 6 VIII 78. (28 V - 6 VIII)

83. *Papilio rutulus* Lucas. Western Tiger Swallowtail.

Widespread, but not very common. Single-brooded with a long flight season. The Western Tiger Swallowtail occurs primarily along creek bottoms within montane coniferous forest, flying far off the ground but dipping down to visit flowers of *Lilium washingtonianum, Rhododendron, Cirsium,* or *Monardella.*

HOST PLANTS: Not known locally.

RECORDS: Canyon Creek, 28 V 77; Scott Valley, 29 V 77; Boulder Creek, 12 VI 76; lower Coffee Creek Canyon, vic. Ranger Station (2), 14 VI 80; Crawford Creek, 15 VI 80; Willow Creek, 16 VI 76; Lone Jack, 18 VI 77; Bridge Camp, 23 VI 76; Mumford Meadow, 25 VI 77; Morris Meadow, 26 VI 76, 4 VIII 79; Yellow Rose Mine Trail, 10 VII 77; Packer's Peak Trail (aberrant), 15 VIII 77. (28 V - 15 VIII)

84. *Papilio multicaudatus* Kirby. Two - Tailed Swallowtail.

We have only two definite records, both at low elevation. These scanty data suggest that *P. multicaudatus* is a bivoltine, foothill species in this area - a picture consistent with other northern California records. However, Emmel and Shields recorded it at mid-elevation in late July, between the foothill dates.

HOST PLANTS: Not known locally.

RECORDS: Scott Valley, 29 V 77; Carrville, 7 VIII 76; recorded by Emmel and Shields from below Brown's Meadow, 20 VII 68.

85. *Papilio eurymedon* Lucas. Pale Swallowtail.

This is a very common and widespread Swallowtail, overall only slightly less numerous than *P. zelicaon.* It is much less regular as a hilltopper than that species. It occurs mostly in canyon bottoms, patrolling along watercourses, or along trails in montane coniferous forest where it may suddenly appear from among the trees. It visits *Vicia, Monardella,* and *Lilium washingtonianum* flowers avidly. Males also frequent puddles and streambanks. There is only one brood, with a very long flight season.

HOST PLANTS: Not determined, but presumably Rhamnaceae.

RECORDS: Canyon Creek (3), 28 V 77; Cecilville, 29 V 77; Crawford Creek (3), 29 V 77, 15 VI 80; Scott Valley, 29 V 77; Boulder Creek (2), 12 VI 76; 6.5 km W Callahan, 15 VI 80; Willow Creek, 16 VI 76; Morris Meadow, 17 VI 76, (2) 26 VI 76; Lone Jack, 18 VI 77; Emerald Lake, 25 VI 76; Coffee Creek, 26 VI 76; Mumford Meadow, 25 VI 77; Hobo Gulch, 18 VII 77; Caribou Lakes trail (2), 10 VIII 76; Union Creek, 6 IX 76. (28 V - 6 IX)

86. *Parnassius clodius* Menetries. Clodius.

Common and widespread. In the lower montane coniferous forest this species is large in size and co-occurs with *Papilio eurymedon, Everes amynthula, Phyciodes orseis, Colias occidentalis, Pieris napi,* etc. along trails and streams. Above 1800 m it is much smaller and occurs in meadows and bogs, where it has a different host. The same sort of variation occurs on the Sierran west slope.

The only virgin female we have seen was taken fresh on 20 September 1979 at Deadfall Lakes, long after the main flight. Presumably there were no males available by then.

HOST PLANTS: Fumariaceae: *Dicentra formosa* (Andr.) Walp. (Crawford Creek); *D. pauciflora* Wats. (Gulick Creek and Mount Eddy).

RECORDS: Crawford Creek, 29 V 77, (3) 15 VI 80; Cecilville (2), 29 V 77; Boulder Creek, 12 VI 76; Mumford Meadow, 14 VI 76, (6) 25 VI 77; Coffee Creek, 800 m (2) 15 VI 80, 1400 m, 26 VI 77; Willow Creek (2), 16 VI 76 (one aberrant, lacks red color); Stuart Fork, 24 VI 76; Morris Meadow, 26 VI 76; Deer Creek (2), 27 VI 76; base of Red Rock Mountain (6), 10 VII 77, 5 IX 76; Gulick Creek, 10 VII 77; Deadfall Lakes (7), 12 VII 79, 6 VIII 78, 16 VIII 79, 20 IX 79; Morgan Meadows (2), 12 VII 79; Grizzly Meadows, 19 VII 77; Gibson Meadows (2) 30 VII 76; Granite Lake, 31 VII 76; Mount Eddy (10), 6 VIII 78; cirque above Josephine Lake, 8 VIII 76; Caribou Basin (3), 9 VIII 76; Brown's Meadow (3), 10 VIII 76; Dorleska Mine, 7 IX 76. (29 V - 20 IX)

87. *Parnassius phoebus sternitzkyi* McDunnough. Sternitzky's Parnassian.

Common, mostly in subalpine and alpine habitats, on sparsely vegetated rocky terrain. This is a hilltopping species, unlike *P. clodius,* and can be very difficult to net on the steep, jagged slopes of the high granite country. In the Caribou Basin it courses over the meadows at the foot of the cliffs. Both sexes visit flowers, especially *Monardella*, and both often bask with wings spread in cool or partly cloudy weather.

There is extensive minor variation.

HOST PLANTS: Crassulaceae: *Sedum obtusatum* Gray ssp. *boreale* Clausen. This plant grows on both granite and ultrabasics and is one of the most characteristic subalpine and alpine plants in the Trinities and Eddies.

RECORDS: Sapphire Lake (2), 25 VI 76; Emerald Lake, 25 VI 76; Granite Lake, 30 VII 76, (5) 31 VII 76; ridge between Deer Creek and Bear Basin, 31 VII 76; Mount Eddy summit area (5), 6 VIII 78, (2) 16 VIII 79, (4) 27 VIII 79, 16 IX 78; Caribou Basin (7), 9 VIII 76; cirque above Josephine Lake, 8 VIII 76; crest of Sawtooth Ridge, 8 VIII 76; Gumboot Butte, 11 VIII 76; Packer's Peak summit, 15 VIII 77; Mirror Lake, 27 VIII 76; Dorleska Summit, 7 IX 76. (25 VI - 16 IX)

HESPERIIDAE

88. *Amblyscirtes vialis* Edwards. Roadside Skipper.

This inconspicuous little skipper occurs in grassy streambank vegetation at mid-elevations in cool canyons, often with *Carterocephalus palaemon*. It may be more widespread than our records indicate.

HOST PLANTS: Presumably Gramineae.

RECORDS: Coffee Creek, 800 m, (3) 14 VI 80; Crawford Creek, 15 VI 80; Stuart Fork below Sawtooth Ridge, 24 VI 76; Coffee Creek, 1400 m, 26 VI 77. (14 VI - 26 VI)

88A. *Euphyes vestris* Boisduval. Dun Skipper.

To our surprise, one fresh female was taken among many *Polites sonora* on the bog at Scott Mountain Summit, 27 VII 80, visiting *Prunella*. The nearest known colonies are in the Hambone-Bartle area and at Mount Shasta City (26 VII 80). It occurs on the west slope of the Coast Ranges in Sonoma and Mendocino Counties.

89. *Paratrytone melane* Edwards. Umber Skipper.

We have two foothill - canyon records. The Trinity-Eddy region is near the northern limit of this species, which is double-brooded throughout its range. The second brood flies several weeks earlier at Sacramento than our Douglas City record.

HOST PLANTS: Unknown.

RECORDS: Coffee Creek, 850 m 27 V 77; Douglas City, 2 X 76.

90. *Ochlodes sylvanoides* Boisduval. Woodland Skipper.

The Woodland Skipper is common in late summer and fall, but it never reaches the enormous abundance often seen at mid-elevations in the western Sierra. Phenotypically our insects resemble North Coast Range ones, but there is extensive variation. High-elevation males are paler and begin to look like Sierran east-slope ones. Visits fall Composites freely. The Woodland Skipper is the commonest butterfly on Rabbitbrush in September in Scott Valley and on the north slope of Mount Shasta.

HOST PLANTS: Presumably Gramineae.

RECORDS: Emerald Lake, 5 VIII 79; Stuart Fork below Sawtooth Ridge (3), 5 VIII 79; Bridge Creek (4), 6 VIII 79; Carrville (3), 7 VIII 76; Packer's Peak (13), 15 VIII 77; Douglas City (12), 29 VIII 79, 2 X 76; Yellow Rose Mine Trail (7), 5 IX 76; Union

Creek Trail (11), 6 IX 76; Dorleska Mine (4), 7 IX 76; Big Flat (15) 7 IX 76, (5) 8 IX 76, (3) 24 IX 77; Deadfall Lakes (17), 16 IX 78, (6) 20 IX 79; Callahan (3) 21 IX 79, 25 IX 77; French Creek (Scott Valley) (6) 21 IX 79; Gazelle (2), 25 IX 77. (5 VIII - 2 X)

91. *Ochlodes agricola* Boisduval. The Farmer.

Two foothill records of a species near its northern limit. Its range largely matches that of California Buckeye, its principal nectar source. Occurs in riparian canyon habitat.

HOST PLANTS: Undetermined.

RECORDS: Lone Jack, 18 VI 77; Hobo Gulch, 18 VII 77.

92. *Atalopedes campestris* Boisduval. The Sachem.

A low-elevation species recorded once as a stray in the Trinities. It also occurs abundantly in autumn in Scott Valley, visiting *Chrysothamnus* flowers. Dornfeld (1980) says it invaded much of Oregon since 1967 and is now firmly established there.

HOST PLANTS: Undetermined; presumably Gramineae.

RECORDS: Callahan (17), 21 IX 79; French Creek (Scott Valley), 21 IX 79; Big Flat, 30 IX 76.

93. *Hesperia juba* Scudder. Yuba Skipper.

Very common in late summer and fall; much less common in spring. As in the Sierra Nevada, spring specimens are usually worn - suggesting that this species, uniquely among American skippers, may hibernate as an adult.

The Yuba Skipper swarms over *Haplopappus bloomeri* and *Chrysothamnus* flowers in September. It is especially numerous on serpentine talus country and in Scott Valley. There is a great deal of minor individual variation.

HOST PLANTS: Presumably Gramineae.

RECORDS: Coffee Creek Canyon, 850 m, 27 V 77; Lone Jack, 28 V 77; Emerald Lake, 25 VI 76; Scott Valley (2), 15 VI 80; Packer's Peak (2), 15 VIII 77; Gulick Creek (5), 5 IX 76; Red Rock Mountain (2), 5 IX 76; Dead Mule Camp (4) 5 IX 76; Union Creek trail (15), 6 IX 76; Dorleska Mine (7), 7 IX 76; slope above Big Flat (4) 7 IX 76; Big Flat (3) 8 IX 76, 25 IX 77; Mount Eddy (2), 16 IX 78; Deadfall Lakes (5), 20 IX 79; Callahan (8), 21 IX 79; French Creek (Scott Valley) (2) 21 IX 79; Douglas City, 2 X 76. (27 V - 25 VI and 15 VIII - 2 X)

94. *Hesperia harpalus* Edwards complex. Harpalus Skipper.

Here belong some of our biggest problems in the Trinity-Eddy fauna. The complex as a whole is common and widespread, but comprises a bewildering array of phenotypically distinctive populations disposed along both elevational and directional gradients.

On the southern and southeastern foothill flank occur almost unmarked Coast Range types (*tildeni* Freeman). Around Mount Shasta City the males are slightly more heavily marked, the females much more so. At high elevations throughout, heavily marked populations with the *oregonia* Edwards pattern in both sexes are found. These descend to the northern foothills (Cecilville) and as close to Mount Shasta City as Morgan Meadows on the southeast side of Mount Eddy. On the north slope of Mount Shasta (Hwy. 97 and Military Pass Road) occur extremely light "desert" *oregonia*. Two similar specimens have been taken among many dark *oregonia* at Deadfall Lakes. Scott Valley *oregonia* are almost as dark as high-elevation ones.

Males of the high-elevation populations are often taken at puddles. Both sexes frequent Rabbitbrush, *Haplopappus*, and *Aster* flowers. Despite the wide spread of dates, there is no evidence of more than one brood anywhere in the area.

HOST PLANTS: Not determined, presumably Gramineae.

RECORDS: *tildeni* phenotypes: Carrville, 730 m (7) 7 VIII 76; Douglas City (4), 29 VIII 79. Light *oregonia*: Mt. Shasta City (4) 31 VIII 77; Schoolhouse Hill, 2 IX 77. Desert (very light) *oregonia*: Military Pass Road (2), 16 VIII 79; Barnes Ranch (Scott Valley), 2 IX 77; Deadfall Lakes (2), 20 IX 79. Dark *oregonia*: Morgan Meadows (10), 12 VII 79; Granite Creek, 30 VII 76; Deadfall Lakes (5) 6 VIII 78, 16 VIII 79, (10) 20 IX 79; Bridge Creek (2) 6 VIII 79; Packer's Peak, 15 VIII 77; Little Castle Lake (2), 22 VIII 77; Parker Creek Divide, 6 IX 76; above Big Flat, 7 IX 76; Big Flat (5), 8 IX 76, 25 IX 77, 30 IX 76; French Creek (Scott Valley) (6) 21 IX 79; Callahan (8), 21 IX 79, (3) 25 IX 77. (12 VII - 30 IX)

95. *Hessperia columbia* Scudder. Columbia Skipper.

Uncommon in the Trinities and Eddies, but fairly frequent in fall in Scott Valley at *Chrysothamnus* with the other *Hesperia*. Apparently double-brooded. Farther south this species is usually associated with foothill chaparral, but we have two records in montane coniferous forest, one on serpentine talus, and a batch from agricultural land (Scott Valley).

HOST PLANTS: Undetermined.

RECORDS: Shadow Creek, 29 V 77; Deer Creek, 27 VI 76; Deadfall Lakes, 20 IX 79; Callahan (4) 21 IX 79; French Creek (Scott Valley) (2), 21 IX 79.

96. *Hesperia lindseyi* Holland. Lindsey's Skipper.

Common from Cecilville to Gazelle, mostly males at mud. Some specimens have little yellow scaling along the veins and are *very* similar to *harpalus*. Their spots are yellower (males), and the early flight season is distinctive. One record also from the south slope.

HOST PLANTS: Unknown.

RECORDS: Lone Jack, 28 V 77; Cecilville, 29 V 77; Crawford Creek (4), 15 VI 80; 11 km E Callahan (8), 15 VI 80; Scott Valley, 15 VI 80; Callahan, 15 VI 80; 6.5 km W Callahan (6), 15 VI 80; 3.2 km W Gazelle, 5 VII 80. (28 V - 5 VII)

97. *Polites sabuleti* Boisduval. Sandhill Skipper.

The Trinity-Eddy populations of the Sandhill Skipper represent a very distinctive, undescribed subspecies which may be characterized as follows: size as large as summer *s. sabuleti* from the Central Valley, never reduced as in *s. tecumseh* Grinnell; ventral hind wing pattern similar to *tecumseh* (males) or darker (females; often with light spots reduced to a curved band and a basal spot on a chocolate ground, resembling *Hesperia harpalus*); *strictly univoltine, flying only in autumn.* This entity is distributed as follows: an isolated colony at Plaskett Meadows, Glenn County (20 collected, 3 IX 76); Trinity-Eddy area at about 1500 m, east to Little Castle Meadow. On the north slope of Mount Shasta univoltine but paler and flying earlier (mid August); at Mount Shasta City possibly intergrading to *P. s. sabuleti* and perhaps biovltine.

"Trinity" *sabuleti* occurs in dry meadows, serpentine barrens, brushy hillsides, and dry creek bottoms. It is probably the commonest butterfly of the region, outnumbering all other butterflies combined during its flight season. It swarms over flowering *Chrysothamnus* and *Haplopappus* in the company of *Hesperia juba* and *H. harpalus* and *Ochlodes sylvanoides*, creating a confusing whirl of small yellow skippers. Perching males are highly territorial, but aggression is suspended at flowers.

HOST PLANTS: Eggs are laid on clumps of *Festuca idahoensis* Elmer (Gramineae) or on bare soil amongst them, and perhaps on other grasses. Larvae are easily reared without diapause on Bermuda Grass. The adult phenotype is constant under high rearing temperature and continuous light.

RECORDS: Deadfall Meadow (2) 16 VIII 79, 27 VIII 79, (22) 20 IX 79; Big Flat (3) 4 IX 76, (10) 8 IX 76, (2) 24 IX 77, (11) 30 IX 76; slope above Big Flat (34), 7 IX 76; Parker Meadow (18) 5 IX 76, (9) 1 X 76; Mumford Meadow (8) 5 IX 76; Parker Creek Trail, 6 IX 76; Dorleska Mine, 7 IX 76; Mount Eddy (3), 16 IX 78. (16 VIII - 1 X)

NOTE: Phenotypes of *sabuleti* from Crater Lake, Oregon, are similar, but these populations fly earlier, 16 VII - 27 VIII (Tilden and Huntzinger, 1977).

98. *Polites sonora* Scudder. Sonora Skipper.

This is a fairly common species on moist meadows and bogs, and is occasional on drier meadows. The ventral hind wing averages little if any darker than in the Sierra, but a few specimens from Mount Eddy and the summit bog on Scott Mountain are noticeably dusky. One brood, earlier than *P. sabuleti*. Visits *Aster*.

HOST PLANTS: Presumably Gramineae.

RECORDS: Eagle Creek (2), 14 VI 80; Coffee Creek, 800 m, 14 VI 80; Crawford Creek, 15 VI 80; Morris Meadow (3) 24 VI 76, 26 VI 76, (2) 4 VIII 79; Mumford Meadow (2), 25 VI 77; meadow at base of Packer's Peak Trail (4), 9 VII 77; bog at Scott Mountain Summit (4), 11 VII 77; Deadfall Lakes (2) 6 VIII 78, (5) 16 VIII 79, (3) 20 IX 79; Mount Eddy, 6 VIII 78; Dead Mule Camp (2), 5 IX 76. (14 VI - 20 IX)

99. *Hylephila phyleus* Drury. Fiery Skipper.

A stray from lower elevations; this species is one of the commonest weedy butterflies in California, almost completely restricted to man - modified habitats where it breeds on Bermuda Grass. The Trinities are near its northern limit. The Big Flat specimen was at *Haplopappus bloomeri*.

HOST PLANTS: Coffee Creek Ranger Station, 27 V 77; Hwy. 3 at Swift Creek, 10 VII 77; Big Flat, 30 IX 76. (27 V - 30 IX)

100. *Carterocephalus palaemon* Pallas. Arctic Skipper.

Frequent in moist, shaded streamside situations in canyons, from the foothills to about 1500 m. Trinity specimens are smaller than those from the well-known colonies in Sonoma and Mendocino Counties. The Arctic Skipper is unrecorded from Mount Eddy, but expected.

HOST PLANTS: Unknown; presumably grasses.

RECORDS: Canyon Creek (7), 28 V 77; Lone Jack, 28 V 77; Cecilville, 29 V 77; Crawford Creek, 29 V 77, 15 VI 80; Coffee Creek, 800 m, 14 VI 80; Stuart Fork below Sawtooth Ridge, 24 VI 76; Emerald Lake (3) 25 VI 76; Deer Creek, 27 VI 76; Morris Meadow, 26 VI 76; Coffee Creek, 1400 m, 26 VI 77. (28 V - 27 VI)

101. *Pholisora catullus* Fabricius. Sooty Wing.

Rather an unexpected casual; a species of disturbed weedy sites where the hosts grow. It occurs in Weaverville and in the dry bed of the Trinity River in summer, but is uncommon.

HOST PLANTS: Elsewhere on Chenopodiaceae and Amaranthaceae.

RECORDS: Lone Jack, 18 VI 77.

102. *Pyrgus ruralis* Boisduval. Montane Checkered Skipper.

Common in open montane to subalpine habitats, especially dry meadows, where it visits Pussy Paws (*Spraguea*). Trinity-Eddy specimens average smaller than Sierran ones, and there are slight but consistent pattern differences. One brood. (Two from Coffee Creek, 1400 m, are very large and unlike the others.)

HOST PLANTS: Rosaceae: *Horkelia fusca* Lindl. ssp. *parviflora* (Nutt.) Keck suspected.

RECORDS: Lone Jack (2), 28 V 77; Lion Lake trail, 13 VI 76; Eagle Creek, 14 VI 80; Union Creek, 14 VI 76; Deadfall Meadow, 15 VI 80; 6.5 km W Callahan, 15 VI 80; Willow Creek Meadow (2), 16 VI 76; Morris Meadow, 17 VI 76, (2) 26 VI 76; Sapphire Lake, 25 VI 76; Emerald Lake (2), 25 VI 76; Mumford Meadow (3) 25 VI 77; Coffee Creek, 1400 m (2), 26 VI 77; Deer Creek, 27 VI 76; base of Red Rock Mountain (2), 10 VII 77; Deadfall Lakes (5) 12 VII 79, (3) 6 VIII 78. (28 V - 6 VIII)

103. *Pyrgus communis* Grote. Common Checkered Skipper.

Frequent on wet to dry meadows on ultrabasic soils. Rare elsewhere. There are at least two broods. Males are extremely territorial; they visit flowers and mud.

These populations do not show the phenotypic oddities of high-altitude Sierran ones, and appear indistinguishable from Central Valley *communis*. Their edaphic restriction reflects the distribution of their hosts.

HOST PLANTS: Malvaceae: *Sidalcea oregana* (Nutt.) Gray ssp. *spicata* (Regel) Hitch. (ova and larvae, Mumford Meadow); *Malva neglecta* Wallr. (larva, Big Flat, 25 IX 77).

RECORDS: Coffee Creek (2), 27 V 77; Mumford Meadow, 14 VI 76, (14) 25 VI 77; Deer Creek, 27 VI 76; 3.2 km W Gazelle, 5 VII 80; Gulick Creek, 10 VII 77; Deadfall Lakes (4) 6 VIII 78, 16 IX 78; Sunrise Creek, 5 IX 76; Deadfall Meadow, 20 IX 79; French Creek (Scott Valley) (2), 21 IX 79. (27 V - 21 IX)

104. *Erynnis icelus* Scudder and Burgess. Dreamy Dusky-wing.

Apparently scarce, but widely distributed around willows at low to mid-elevations. Often found at puddles.

HOST PLANTS: Willows suspected.

RECORDS: Canyon Creek (2), 28 V 77; Lone Jack, 28 V 77; Scott Valley (2), 29 V 77; Coffee Creek, 800 m, 14 VI 80; Crawford Creek (2), 15 VI 80; 11 km E Callahan (2), 15 VI 80; Callahan, 15 VI 80. (28 V - 15 VI)

105. *Erynnis propertius* Scudder and Burgess. Propertius Dusky-wing.

Abundant and general where oaks occur; straying to above tree line. This species is probably single-brooded in our region, but has a very long flight season. It is a frequent visitor to *Monardella* flowers and to mud puddles. Males are highly territorial.

HOST PLANTS: Fagaceae: *Quercus garryana* Dougl. (Oregon Oak), probably other Oaks.

RECORDS: Lone Jack, 28 V 77; Canyon Creek (2), 28 V 77; Shadow Creek, 29 V 77; Scott Valley, 29 V 77; Cecilville, 29 V 77; Boulder Creek (2), 12 VI 76, 14 VI 76; Lion Lake trail, 13 VI 76; Union Creek, 14 VI 76; Coffee Creek, 800 m, 14 VI 80; Eagle Creek, 14 VI 80; lower Bear Basin Meadow, 15 VI 76; Crawford Creek, 15 VI

80; 11 km E Callahan, 15 VI 80; Callahan, 15 VI 80; 6.5 km W Callahan, 15 VI 80; Morris Meadow, 17 VI 76, 26 VI 76; Mumford Meadow (3) 25 VI 77; Emerald Lake, 25 VI 76; Coffee Creek, 1400 m, 26 VI 77; 3.2 km W Gazelle, 5 VII 80; Sunrise Pass (2), 10 VII 77; Deadfall Lakes, 12 VII 79; Mount Eddy summit (2), 6 VIII 78; upper Caribou Lakes Trail, 2000 m, 10 VIII 76; Gumboot Butte, 2048 m, 11 VIII 76. (28 V - 11 VIII)

106. *Erynnis pacuvius* Lintner. Pacuvius Dusky-Wing.

Uncommon. Our series, mostly from mud puddles, is too short for a confident subspecific determination. Geographically speaking, these should be *lilius* Dyar.

HOST PLANTS: Undetermined. *Ceanothus* spp. elsewhere.

RECORDS: Coffee Creek, 800 m, 14 VI 80; Eagle Creek (4), 14 VI 80; Coffee Creek, 1400 m, (2) 26 VI 77. (14 VI - 26 VI)

107. *Erynnis persius* Scudder. Persius Dusky-wing.

Persius is fairly widespread on dry meadows, mostly on ultrabasic soils in the Trinity-Eddy area. Like its relatives, it visits mud puddles; the autumn brood visits *Aster* and *Haplopappus bloomeri*. This is the only fully double-brooded Dusky-wing in the Trinities and Eddies.

HOST PLANTS: Unknown.

RECORDS: Canyon Creek (2), 28 V 77; Lone Jack, 28 V 77; Coffee Creek, 850 m, 29 V 77, 14 VI 80; Lion Lake trail, 13 VI 76; Crawford Creek, 15 VI 80; Mumford Meadow (4), 25 VI 77; Parker Meadow, 21 VIII 77; Dead Mule Camp, 5 IX 76; slope above Big Flat, 7 IX 76; Deadfall Lakes (4), 16 IX 78. (28 V - 16 IX)

108. *Thorybes pylades* Scudder. Northern Cloudy-wing.

Frequent, foothills to montane meadows, mostly in canyon riparian habitat, visiting flowers. This is the lowest-elevation member of the genus.

HOST PLANTS: Associated with *Lathyrus jepsonii* ssp. *californicus* (Wats.) Hitchc. at Morris Meadow, its highest station.

RECORDS: Coffee Creek, 850 m, 27 V 77, 800 m 14 VI 80; Canyon Creek, 28 V 77; Lone Jack, 28 V 77; Crawford Creek, 29 V 77, 15 VI 80; Scott Valley, 29 V 77; Morris Meadow (2), 26 VI 76. (27 V - 26 VI)

109. *Thorybes diversus* Bell. Scarce Cloudy-wing.

Rare. Thus far recorded only once, at the edge of a large sedgy meadow, sipping mud with the next species. A number of collectors have mistakenly reported *diversus* from the Trinity-Eddy area through confusion with *T. m. aemilia*. It may be recognized by the very plain, dark brown hind wing beneath, virtually lacking the dark bars and fine striations characteristic of *aemilia*.

In the Sierra Nevada, *diversus* is a mid-elevation species often found in small clearings rather than the large meadows.

HOST PLANTS: Unknown locally.

RECORDS: Mumford Meadow (3), 25 VI 77.

110. *Thorybes mexicana aemilia* Skinner. Emily's Cloudy-wing.

Emily's Cloudy-wing has long been confused with both the preceding species and with *T. m. nevada* Scudder of the Sierra Nevada. It differs from the latter in having a more boldy marked ventral hind wing often tinged with yellowish, and a usually more complete pattern of white spots on the fore wing (as figured in the last edition of Holland's *Butterfly Book*). Mount Eddy specimens are slightly larger and darker than Trinity ones and are closer to a series from Three Creeks Meadows, 27 km S. Sisters, Deschutes Co., Oregon, sent by J. Hinchliff; Trinity ones are perhaps the most aberrant in the *mexicana* complex.

This is a very common to abundant species in the higher montane and subalpine meadows and bogs, mainly on ultrabasics; it is associated with *Phyciodes campestris, Agriades glandon*, etc. It does not seem to hilltop in the Trinities, but we have it from the very top of Mount Eddy.

HOST PLANTS: Unknown, but closely associated with *Trifolium* on the meadows.

RECORDS: Mumford Meadow, 14 VI 76, (18) 25 VI 77; Deadfall Meadow, 15 VI 80; Deer Creek, 16 VI 76, 27 VI 76; Morris Meadow (2), 17 VI 76, 24 VI 76, 26 VI 76; Gulick Creek (4), 10 VII 77; Deadfall Lakes (6), 12 VII 79, 16 VIII 79; Mount Eddy summit area (5), 6 VIII 78. (14 VI - 16 VIII)

111. *Epargyreus clarus* Cramer. Silver-Spotted Skipper.

Occasional in foothill and lower montane canyons. Common in Weaverville, where its naturalized host plant, *Robinia*, is used as a street tree. One brood. An avid visitor to flowers, especially Red Clover.

HOST PLANTS: Unknown in Trinities; at Weaverville, *Robinia*; usually on *Amorpha*.

RECORDS: Lone Jack, 28 V 77; Cecilville, 29 V 77; Eagle Creek, 14 VI 80; Coffee Creek, 800 m, (3) 14 VI 80, 1400 m, 26 VI 77; Hobo Gulch, 18 VII 77. (28 V - 18 VII)

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Fig. 3. Locations of Californian faunas compared in Tables 1-4. a, Trinity Alps; b, Mount Eddy; c, Yuba Pass; d, South Yuba River Country (Lang, Donner, Castle); e, Yosemite National Park, including Tioga Pass.

Table 1

Faunas of eight areas, drawn from various sources. The South Yuba River Country, parallel to Interstate 80, contains three subunits: Lang Crossing (montane, ca. 1500 m, including both xeric and mesic habitats), Donner Pass (high montane - subalpine, 2100 m), and Castle Peak (subalpine - alpine, 2700 m). Castle Peak is The next-to-last 2700 m peak in the northern Sierra (Shapiro, 1977). Tioga Pass is listed separately even though it is included in the Yosemite fauna, because it is the best-documented alpine fauna in the High Sierra. Clinal and otherwise ambiguous subspecies are generally omitted.

	Crater Lake National Park[1]	Trinity Alps + Mount Eddy[2]	Yuba Pass - Gold Lake Area[3]	South Yuba River Country[4]			Yosemite National Park[5]	Tioga Pass[6]
				Castle Peak	Donner Pass	Lang Crossing		
Danaus plexippus	x	x	x		x	x	x	x
Danaus gilippus							x	
Coenonympha tullia california			x		x	x	x	
ampelos			x		x			
mono							x	
eryngii	x	x						
Cercyonis pegala ariane							x	
boopis	x	x	x					
Cercyonis sthenele silvestris		x	x			x	x	
Cercyonis oeta	x			x	x		x	x
Oeneis ivallda				x	x		x	x
Oeneis nevadensis	x	x						
Speyeria cybele leto		x	x		x	x	x	
S. nokomis apacheana							x	
S. zerene zerene			x		x	x	x	
conchyliatus	x	x						
malcolmi							x	
S. callippe inornata			x		x	x	x	
nevadensis							x	
rupestris		x						
semivirida	x							
S. egleis egleis			x	x	x		x	x
oweni	x	x						
S. hydaspe hydaspe			x		x	x	x	
purpurascens	x	x						
S. atlantis irene			x		x		x	
dodgei	x	x						
S. coronis snyderi			x		x	x		
simaetha	x	x						
S. mormonia arge			x		x		x	x
erinna	x	x						
Boloria epithore	x	x	x		x	x	x	x
Euphydryas chalcedona chalcedona/ truckeensis		x	x			x	x	
sierra							x	
uncertain ssp.		x						

	Crater Lake National Park[1]	Trinity Alps + Mount Eddy[2]	Yuba Pass - Gold Lake Area[3]	South Yuba River Country[4]			Yosemite National Park[5]	Tioga Pass[6]
				Castle Peak	Donner Pass	Lang Crossing		
Euphydryas editha rubicunda							x	
nubigena + *aurilacus*			x				x	x
monoensis							x	
lawrencei	x							
colonia		x						
uncertain ssp.		x						
Chlosyne damoetas malcolmi							x	x
C. acastus							x	
C. palla	x	x	x		x	x	x	
C. hoffmanni hoffmanni				x	x		x	
segregata	x	x						
C. leanira		x	x				x	
Phyciodes campestris campestris	x	x					x	
montana			x	x	x	x	x	x
"Great Basin"							x	
P. orseis orseis		x						
herlani					x			
P. mylitta	x	x	x		x	x	x	x
Polygonia satyrus		x				x	x	
P. faunus rusticus	x	x			x	x	x	
P. zephyrus	x	x	x	x	x	x	x	x
Nymphalis milberti	x	x	x	x	x	x	x	x
N. californica	x	x	x	x	x	x	x	
N. antiopa	x	x	x		x	x	x	x
Vanessa annabella	x	x	x	x	x	x	x	
V. atalanta	x	x	x		x	x	x	x
V. virginiensis	x	x	x	x	x	x	x	
V. cardui	x	x	x	x	x	x	x	x
Precis coenia	x	x	x	x	x	x	x	x
Limenitis lorquini	x	x	x		x	x	x	
Limenitis weidemeyerii							x	
Adelpha bredowii californica	x	x	x		x	x	x	
Apodemia mormo mormo		x			x	x	x	
tuolumnensis							x	
Habrodais grunus	x	x	x		x[7]	x	x	
Atlides halesus				x[7]		x	x	
Strymon melinus		x	x		x	x	x	
Satyrium fuliginosum fuliginosum				x	x		x	
"Trinity"		x						
Satyrium behrii	x		x		x		x	
S. auretorum			x			x	x	

					South Yuba River Country[4]			
	Crater Lake National Park[1]	Trinity Alps + Mount Eddy[2]	Yuba Pass - Gold Lake Area[3]	Castle Peak	Donner Pass	Lang Crossing	Yosemite National Park[5]	Tioga Pass[6]
S. saepium	x	x	x		x	x	x	
S. tetra							x	
S. sylvinus (incl. *dryope*)		x	x		x	x	x	
S. californica	x	x	x		x	x	x	
Callophrys dumetorum		x				x	x	
C. lemberti	x	x	x	x	x	x	x	x
Mitoura spinetorum	x	x	x		x		x	
M. johnsoni			x				x	
M. nelsoni	x	x	x		x[7]	x	x	
Incisalia fotis complex			x		x	x	x	
I. iroides	x	x	x		x	x	x	
I. eryphon	x	x	x	x[7]	x	x	x	
Lycaena arota arota		x	x		x	x	x	
virginiensis					x		x	
L. gorgon		x	x				x	
L. heteronea	x	x		x	x		x	x
L. xanthoides							x	
L. editha	x		x	x	x	x	x	x
L. rubidus			x		x		x	x
L. mariposa	x	x	x	x	x		x	x
L. nivalis nivalis			x	x	x	x	x	x
"Trinity" [8]	x	x						
L. helloides	x	x	x		x	x	x	x
L. phlaeas hypophlaeas							x	
L. cupreus	x		x	x	x	x	x	x
Leptotes marina					x[7]		x	
Brephidium exilis					x[7]	x[7]	x	
Hemiargus isola					x[7]		x	x[7]
Lycaeides argyrognomon anna + *ricei*	x	x	x		x	x	x	x
Lycaeides melissa melissa		x	x		x			
inyoensis							x	
Agriades glandon podarce	x	x	x		x		x	x
Plebeius saepiolus	x	x	x	x	x	x	x	x
P. icarioides icarioides	x	x	x	x	x	x	x	
fulla							x	
P. shasta	x			x	x		x	x
P. acmon		x	x	x	x	x	x	
P. lupini	x	x	x	x	x	x	x	x
Everes comyntas							x	
E. amyntula (montane)	x	x	x		x	x	x	
alpine		x		x				
Euphilotes enoptes		x	x	x	x	x	x	x

				South Yuba River Country[4]				
	Crater Lake National Park[1]	Trinity Alps + Mount Eddy[2]	Yuba Pass - Gold Lake Area[3]	Castle Peak	Donner Pass	Lang Crossing	Yosemite National Park[5]	Tioga Pass[6]
Euphilotes battoides battoides							x	
oregonensis	x							
glaucon							x	
intermedia		x	x		x	x		x
E. speciosa							x	
Philotes sonorensis			x			x		
Glaucopsyche piasus	x	x				x	x	
G. lygdamus	x	x	x	x	x	x	x	x
Celastrina argiolus echo	x	x	x	x	x	x	x	x
Anthocharis sara sara		x				x	x	
stella			x	x	x		x	
flora	x							
A. lanceolata		x	x			x	x	
Euchloe hyantis		x	x	x	x	x	x	
E. ausonides		x		x		x	x	
Colias eurytheme	x	x	x	x	x	x	x	x
C. philodice eriphyle		x			x		x	
C. occidentalis chrysomelas		x	x				x?	
C. behrii							x	x
Zerene eurydice							x	
Nathalis iole							x	
Neophasia menapia	x	x	x		x	x	x	
Pieris beckerii	x	x			x		x	
P. sisymbrii	x	x	x	x	x	x	x	x
P. protodice	x	x			x	x	x	
P. occidentalis	x	x	x	x	x	x	x	x
P. napi microstriata			x			x	x	
uncertain ssp.	x	x						
P. rapae	x	x	x		x	x	x	
Battus philenor			x[7]					
Papilio zelicaon	x	x	x	x	x	x	x	x
P. indra		x	x	x	x		x	x
P. rutulus	x	x	x		x	x	x	x
P. multicaudatus		x				x	x	
P. eurymedon	x	x	x	x	x	x	x	x
Parnassius clodius	x	x	x	x	x	x	x	x
P. phoebus behrii							x	x
sternitzkyi		x						
Epargyreus clarus		x	x			x	x	
Pholisora catullus		x[7]			x[7]	x		
Thorybes pylades		x				x	x	
T. mexicana nevada			x	x	x	x	x	x
aemilia	x	x						

				South Yuba River Country[4]				
	Crater Lake National Park[1]	Trinity Alps + Mount Eddy[2]	Yuba Pass - Gold Lake Area[3]	Castle Peak	Donner Pass	Lang Crossing	Yosemite National Park[5]	Tioga Pass[6]
T. diversus		x				x	x	
Pyrgus ruralis	x	x	x	x	x	x	x	
P. communis		x	x	x	x	x	x	
Heliopetes ericetorum			x			x	x	
Erynnis persius	x	x	x		x	x	x	
E. icelus	x	x	x			x		
E. pacuvius lilius	x	x	x			x	x	
E. propertius		x	x	x[7]	x	x	x	
E. zarucco funeralis							x	
Hesperia miriamae							x	x
H. nevada				x	x		x	
H. juba	x	x	x	x	x	x	x	x
H. columbia		x						
H. lindseyi		x						
H. harpalus harpalus			x	x	x		x	x
yosemite			x		x	x	x	
tildeni		x						
oregonia	x	x						
Ochlodes sylvanoides	x	x	x		x	x	x	
O. agricola		x	x			x	x	
Polites sabuleti sabuleti					x[7]		x	
tecumseh				x	x	x	x	x
"Trinity"	x	x						
P. sonora	x	x	x		x	x	x	x
Hylephila phyleus		x[7]			x[7]	x[7]		
Atalopedes campestris		x			x[7]	x		
Lerodea eufala						x[7]		
Paratrytone melane		x					x	
Amblyscirtes vialis		x	x		x	x	x	
Carterocephalus palaemon	x	x	x					
Total taxa:	80	116	99	48	102	96	148	50

Notes: [1] Tilden and Huntzinger 1977 plus museum records and Dornfeld 1980

[2] Present study

[3] Opler, unpublished; Shapiro, unpublished

[4] Shapiro, unpublished data

[5] Garth and Tilden 1963 plus O. Shields notes

[6] Tilden 1959 plus O. Shields notes

[7] definitely non-resident; strays

[8] Dornfeld's (1980) "form 1"

Table 2

Resemblances among the faunas in Table 1.

Above diagonal: Numbers of shared taxa

Below diagonal: Sørensen's coefficient

	Crater	Trinity	Yuba	Castle	Donner	Lang	Yuba River (C+D+L)	Yosemite	Tioga
Crater		71	54	29	57	51	60	59	31
Trinity	0.724		71	31	69	76	83	83	31
Yuba	0.603	0.660		37	80	78	90	90	40
Castle	0.453	0.378	0.503		45	35		47	32
Donner	0.615	0.633	0.796	0.600		75		94	45
Lang	0.579	0.731	0.800	0.486	0.758			88	33
Yuba River (C+D+L)	0.588	0.667	0.807					112	46
Yosemite	0.502	0.629	0.725	0.480	0.752	0.721	0.823		
Tioga	0.477	0.374	0.537	0.653	0.592	0.452	0.529		

Crater		0.568	0.432	0.293	0.456	0.408	0.417	0.349	0.313
Trinity	0.888		0.493	0.233	0.463	0.559	0.529	0.459	0.230
Yuba	0.675	0.717		0.336	0.661	0.667	0.677	0.573	0.367
Castle	0.604	0.646	0.771		0.429	0.321		0.315	0.485
Donner	0.713	0.677	0.808	0.938		0.610		0.603	0.421
Lang	0.638	0.792	0.813	0.729	0.781			0.564	0.292
Yuba River (C+D+L)	0.750	0.716	0.909					0.700	0.359
Yosemite	0.738	0.712	0.909	0.979	0.922	0.917	0.903		
Tioga	0.620	0.620	0.800	0.667	0.900	0.660	0.920		

Above diagonal: Jaccard's coefficient of community

Below diagonal: Simpson's index

Table 3

"Hudsonian" and "Arctic-Alpine" butterfly species recorded in four areas.

	Yosemite[1]	Donner-Castle[2]	Trinity Alps[3]	Mount Eddy[3]
Cercyonis oeta	x	x		
Oeneis ivallda	x	x		
Speyeria egleis egleis	x	x		
oweni			x	x
Speyeria mormonia arge	x	4		
erinna				x
Boloria epithore	x	x	x	x
Euphydryas editha nubigena	x			
colonia			x	
Euphydryas chalcedona ssp.			x	
Chlosyne damoetas malcolmi	x			
Chlosyne palla	x			
Phyciodes campestris campestris			x	x
montana	x	x		
Polygonia zephyrus	x	x	x	x
Nymphalis californica	x	x	x	x
Nymphalis milberti	x	x	x	x
Nymphalis antiopa	x	x	x	x
Vanessa cardui	x	x	x	x
Vanessa annabella	x	x	x	x
Vanessa virginiensis		x	x	x
Apodemia mormo mormo	x		x	x
Callophrys lemberti	x	x	x	x
Satyrium fuliginosum fuliginosum		x		
"Trinity"			x	x
Incisalia eryphon	x	x		
Incisalia iroides			x	
Lycaena heteronea	x	x	x	x
Lycaena rubidus	x			
Lycaena editha	x	x		
Lycaena mariposa	x	x	x	x
Lycaena nivalis nivalis	x	x		
"Trinity"[5]			x	x
Lycaena phlaeas hypophlaeas	x			
Lycaena cupreus	x	x		
Lycaeides argyrognomon	x	x	x	x
Lycaeides melissa melissa			x	x
inyoensis	x			
Agriades glandon podarce	x	x	x	x
Plebeius saepiolus	x	x	x	x
Plebeius icarioides		x		
Plebeius shasta	x	x		
Plebeius acmon	x	x	x	x
Plebeius lupini	x	x	x	x
Everes amyntula		x	x	x

	Yosemite[1]	Donner-Castle[2]	Trinity Alps[3]	Mount Eddy[3]
Euphilotes enoptes	x	x	x	x
Euphilotes battoides	x			
Glaucopsyche lygdamus	x	x	x	x
Celastrina argiolus echo		x		
Euchloe ausonides	x	x	x	
Euchloe hyantis		x	x	x
Anthocharis sara stella		x		
Colias eurytheme	x	x	x	x
Colias behrii	x			
Pieris sisymbrii	x	x	x	x
Pieris occidentalis	x	x	x	x
Papilio zelicaon	x	x	x	x
Papilio indra	x	x	x	x
Parnassius clodius	x	x	x	x
Parnassius phoebus behrii	x			
sternitzkyi			x	x
Thorybes mexicana nevada	x	x		
aemilia			x	x
Pyrgus communis		x	x	x
Pyrgus ruralis		x		
Hesperia miriamae	x			
Hesperia nevada		x		
Hesperia juba	x	x	x	x
Hesperia harpalus harpalus	x	x		
oregonia			x	x
Polites sabuleti tecumseh	x	x		
"Trinity"			x	x
Polites sonora	x	x	x	x
Total taxa:	51	48	43	40

Notes:[1] Garth and Tilden 1963

[2] Shapiro, unpublished and 1977

[3] Present study

[4] residency not established; common in montane zone

[5] Dornfeld's (1980) "form 1"

Table 4

Resemblances among the faunas in Table 3.

Above diagonal: Numbers of shared taxa

Below diagonal: Sørensen's coefficient

	Yosemite	Donner-Castle	Trinity Alps	Mount Eddy
Yosemite		38	28	26
Donner-Castle	0.768		29	30
Trinity Alps	0.596	0.637		39
Mount Eddy	0.571	0.682	0.939	

	Yosemite	Donner-Castle	Trinity Alps	Mount Eddy
Yosemite		0.623	0.424	0.400
Donner-Castle	0.792		0.468	0.517
Trinity Alps	0.651	0.675		0.886
Mount Eddy	0.650	0.750	0.975	

Above diagonal: Jaccard's coefficient of community

Below diagonal: Simpson's index

Table 5

Seasonal distribution of butterflies collected and seen in the montane, subalpine, and alpine Trinity Alps in 1976.

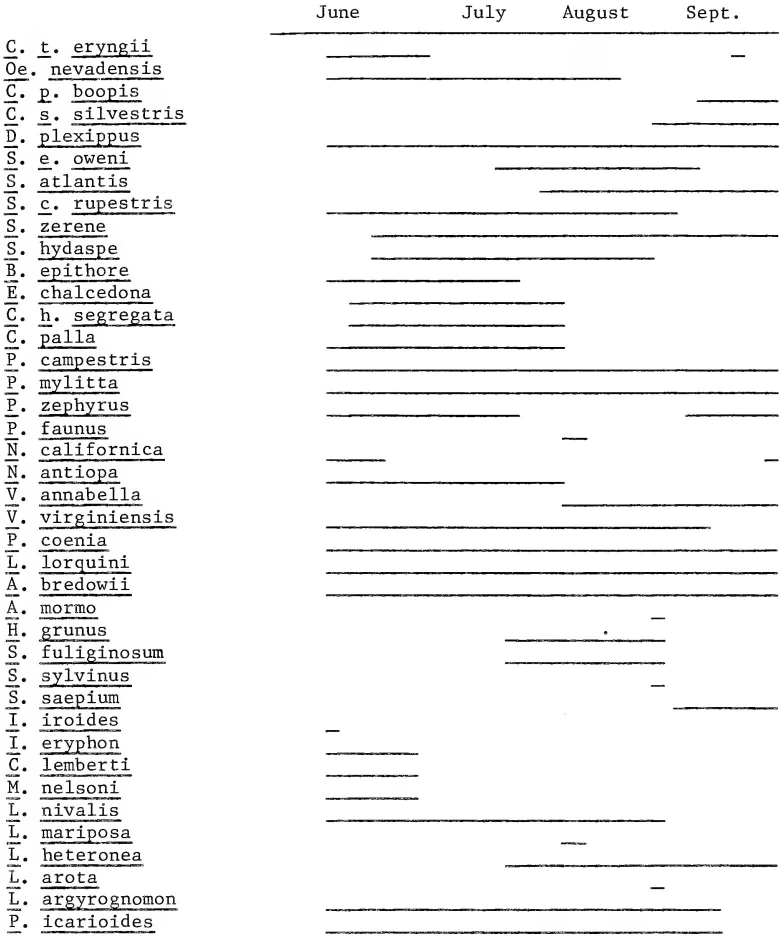
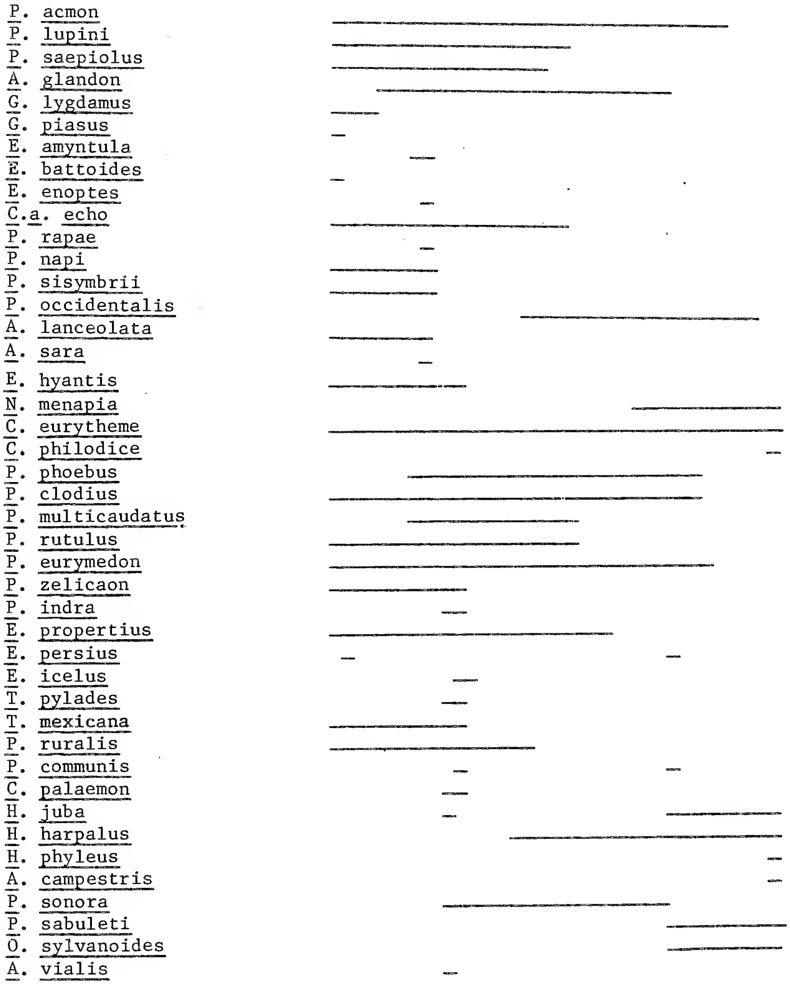


Table 5

Seasonal distribution of butterflies collected and seen in the montane, subalpine, and alpine Trinity Alps in 1976.



Appendix I

List of Trinity-Eddy Localities

All are mapped on the Redding and Weed sheets of the USGS 1:250,000 series. Topo maps (15′ series) indicated by the following abbreviations: BK - Bonanza King; CC - Coffee Creek; ET - Etna; WV - Weaverville; TD - Trinity Dam; CEC - Cecilville; W - Weed; CM - China Mountain; HEL - Helena. Elevations approximate.

Bear Basin: NE of Seven-Up Peak; drains to Swift Creek via Bear Creek. 1800-2120 m. CC

Big Flat: major campground - trailhead on Coffee Creek Road at 1500 m. CC

Black Basin: NW of Seven-Up Peak, drains to Deer Creek. 1970-2273 m. CC

Black Mountain: Major hilltopping site S of Red Rock Mt., looking down on Ward Lake and upper Sunrise and Swift Creeks. 2430 m. CC

Bob's Farm: 4 km W of Upper Grizzly Meadows. 1620 m. CEC

Boulder Creek: Cub Wallow, 2211 m, to Coffee Creek, 900 m; deep V-shaped canyon open to N. CC (There is another Boulder Creek, 1500-1970 m, vic. Mount Hilton.)

Bridge Camp: Trailhead, lower Stuart Fork, 800 m. TD

Brown's Meadow: on Caribou Lakes Trail (new) NE of Little Caribou Lake; 1939 m. CC

Callahan: Jct. Scott River and Noyes Valley Creek, Hwy. 3, 32 km NNE of Big Flat, 875 m. Extensive Rabbitbrush in autumn. ET

Canyon Creek: Hwy. 299 to Canyon Creek Lakes (600-1725+ m), most collections above Ripstein Camp (900 m). South slope major canyon. HEL

Caribou Basin: 2120 m; N side Sawtooth Ridge, upper and lower Caribou Lakes, Snowslide Lake. Very cold subalpine basin with bogs and meadows on granite. CC

Caribou Lakes Trail (new): Big Flat (1500 m) to Caribou Lakes (2460 m), over flank of Caribou Mountain. Montane chaparral, coniferous forest, *Cercocarpus*, bogs. CC

Carrville: 731 m; serpentine chaparral on Hwy. 3, N end Trinity (Clair Engle) Lake. TD

Cecilville: montane coniferous forest; S Fork Salmon River, 695 m, North slope. CEC

Coffee Creek: Ranger Station, 725 m, to Carter's Resort, 1600 m; includes Big Flat. CC

Cold Spring: Stuart Fork near lower end Morris Meadows, 1268 m. TD

Crawford Creek: 1.6 km NE Cecilville (725-1450 m). CEC

Deadfall Lakes: 2180-2364 m; in basin surrounded by "arms" of Mount Eddy; boggy, subalpine. CM, W

Dead Mule Camp: upper end Parker Meadow (Swift Creek), 1545 m. CC

Deer Creek: Morris Meadow to Deer Lake, 1322-2300 m. TD

Dorleska Mine: 2060 m; below Preacher's Peak; tailings, *Eriogonum, Chrysothamnus*. CC

Dorleska Summit: 2135 m, just S of Preacher's Peak, above Yellow Rose Mine; colony of subalpine *Purshia*, unusual mineralogy. CC

Douglas City: 500 m; 18.2 km S Weaverville; foothill. WV

Mount Eddy: 2738 (or 2750) m; highest ultrabasic point in state; 14.4 km WNW Mt. Shasta City; alpine. W, CM

Emerald Lake: upper Stuart Fork drainage, granite, pink heather, subalpine, 1667 m. CC

Foster's Cabin: at Dead Mule Camp, Swift Creek, 1545 m. CC

Foster Lake: near Lion Lake; a source of Union Creek. 2300 m. CC

Gazelle: 16 km W Dwinnell Reservoir, NW of Mt. Shasta, 834 m. I-5 at Callahan-Gazelle Road. Great Basin, irrigated alfalfa.

Gibson Meadows: just below Granite Lake, 1750 m. TD

Granite Creek: drains into Swift Creek; rises from a very low, N-facing snowfield; 2212-1212 m. TD

Granite Lake: on Granite Creek, 1818 m. Granite and ultrabasic slopes. TD

Grizzly Lake: below the Thompson Peak icefield (2728 m), alpine, bare granite (2152 m). CEC

Grizzly Meadows: (upper and lower) 1697-1939 m, Grizzly Creek N of lake; boreal. CEC

Gulick Creek: opposite Red Rock Mountain. Boggy, ultrabasic talus. 2030-1667 m. CC

Gumboot Butte and Lake: 2048-1879 m; subalpine ultrabasics in Trinity Divide, 11.2 km E Hwy. 3. BK

Hobo Gulch: North Fork Trinity River below Backbone Ridge on route to Papoose Lake, 909 m. HEL

Josephine Lake: NE side of Sawtooth Ridge above Carter's Resort. Unnamed cirque at 2120 m above Lake. CC

Lion Lake Trail: from Boulder Creek (1660 m) to 2120 m. CC

Little Salt Creek: Tributary of Stuart Fork, rising from Siligo Peak (2473 m), collected 1152-1788 m. TD

Lone Jack: Foot of Noonan Gulch, E Fork Trinity River, 636 m, 10.4 km N Helena. HEL

Martin Gulch Fork: off Rattlesnake Creek, 8 km NW Papoose Lake, 1091-1364 m. CEC

Mirror Lake: Hanging lake above Sapphire Lake, source of Stuart Fork. 2000 m. CEC

Morris Meadow: very large meadows, wet and dry, on Stuart Fork, 1333-1430 m. TD

Morgan Meadows: E side Mt. Eddy, 1500 m. W

Mumford Meadow: large meadow on Swift Creek, 1606-1727 m. CC

Packers Peak: Above Big Flat. Summit 2387 m. CC

Papoose Lake Trail: from Backbone Creek to Papoose Lake, 900-2025 m. HEL

Parker Creek Trail: from Parker Meadow to Parker Creek Divide (2100 m), ultrabasic, steep. CC

Parker Meadow: large meadow on Swift Creek, 1515-1545 m. CC

Red Rock Mountain: Summit 2395 m. Highest point in Red Trinities. Alpine, overlooking Sunrise Pass. CC

Sapphire Lake: 1818 m; above Emerald Lake; subalpine granite. CC

Sawtooth Ridge: divide between Stuart Fork and Caribou Basin; crest 2408 m; major hilltop area, snowfields on N side. CC, TD

Scorpion Creek: W side Bonanza King opposite just N of Coffee Creek mouth, 900-1700 m. BK

Scott Mountain: Hwy. 3 between Callahan and Trinity Center. Ultrabasic, with bog near summit at 1500+ m. CM

Scott Valley: NNW of Callahan; Rabbitbrush abundant especially at French Creek (875 m). ET

Shadow Creek: 9.5 km NE Cecilville; 865-1620 m. CEC

Stuart Fork: Bridge Camp to Emerald Lake (800-1667 m). TD

Sunrise Creek: Sunrise Pass to Swift Creek; ultrabasic; bog. 1695-2060 m. CC

Sunrise Pass: S of Red Rock Mountain; head of Sunrise Creek; high subalpine, Foxtail Pine. 2120 m. CC

Swift Creek: Hwy. 3 to Horseshoe Lake (738 to 2182 m) via Mumford & Parker Meadows. Lower part forested. CC

Thompson Peak: Highest point in Trinities (2744 m); alpine granite, snowfields. CEC

Trinity Summit: French Gulch Road, lower montane coniferous forest (1152 m).

Union Creek Trail: Union Lake (1848 m) to Coffee Creek (1272 m), headwaters at Parker Creek Divide (2100 m). Ultrabasic, bogs, moraines. CC

Willow Creek: 1970-1600 m; tributary of Deer Creek, 3.2 km NW Morris Meadow. TD

Yellow Rose Mine Trail: Big Flat (1500 m) to Sunrise Pass (2120 m). Includes oak scrub, mine tailings; above Gulick Creek. CC

Appendix II

Species Lists for Trips after Mid-VII 1980

Deadfall Lakes, 24 VII 80:

Oe. nevadensis, S. egleis oweni, B. epithore, C. hoffmanni segregata, P. campestris, N. californica (hibernators), *P. coenia, L. lorquini, L. nivalis, I. eryphon, C. lemerti, E. enoptes, P. icarioides, P. saepiolus, C. eurytheme, P. sisymbrii, P. occidentalis, P. rapae, E. hyantis, P. zelicaon, P. clodius, P. sonora, P. ruralis,*

Mt. Eddy above upper Deadfall Lakes, 26 VII 80:

Oe. nevadensis, S. egleis oweni, L. heteronea, C. lemberti, L. argyrognomon, P. saepiolus, P. lupini, C. eurytheme, P. sisymbrii, P. occidentalis, P. zelicaon, P. eurymedon, P. clodius, P. phoebus sternitzkyi, H. harpalus oregonia, E. propertius.

Deadfall Meadow, 26 VII 80:

S. atlantis, B. epithore, C. hoffmanni segregata, P. campestris, P. orseis, P. mylitta, P. zephyrus, L. lorquini, L. nivalis, E. battoides, C. argiolus echo, L. argyrognomon, P. saepiolus, P. icarioides, A. glandon, E. amyntula, C. eurytheme, P. occidentalis, P. zelicaon, P. eurymedon, P. clodius, P. sonora, P. communis, E. propertius, T. mexicana aemilia.

Yellow Rose Mine Trail to Sunrise Pass, 27 VII 80:

Oe. nevadensis, C. sthenele silvestris, S. atlantis, S. egleis oweni, S. hydaspe, C. hoffmanni segregata, E. chalcedona (subalpine), *P. campestris, P. zephyrus* (hibernator), *V. virginiensis, L. lorquini, L. nivalis, L. mariposa, H. grunus, S. saepium, S. fuliginosum, M. nelsoni, G. piasus, G. lygdamus, C. argiolus echo, P. saepiolus, P. lupini, A. glandon, P. sisymbrii, P. occidentalis, P. rapae, E. ausonides, P. zelicaon, P.*

indra, P. eurymedon, P. clodius, P. phoebus sternitzkyi, P. sonora, P. ruralis, E. propertius, T. mexicana aemilia.

Coffee Creek Ranger Station, 27 VII 80:

Oe. nevadensis, C. sthenele silvestris, P. rutulus, P. rapae, H. harpalus near *tildeni.*

Scott Mountain summit, 27 VII 80:

C. sthenele silvestris, S. atlantis, B. epithore, P. campestris, V. annabella, L. mariposa, L. argyrognomon, P. saepiolus, P. lupini, A. glandon, C. eurytheme, N. menapia, P. clodius, E. vestris, P. sonora, P. ruralis, E. propertius.

Coffee Creek canyon, ca. 1200-1400 m, 27 VII 80:

Oe. nevadensis, C. sthenele silvestris, S. callippe rupestris, S. hydaspe, P. mylitta, P. satyrus, N. californica, V. virginiensis, P. coenia, L. lorquini, A. bredowii, L. arota, S. sylvinus, M. nelsoni, E. enoptes, P. acmon, C. eurytheme, P. rapae, P. rutulus, P. eurymedon,P. clodius, O. sylvanoides, H. harpalus oregonia, P. sonora, E. propertius, E. pacuvius, T. mexicana aemilia.

Mt. Eddy, 15 VIII 80:

S. atlantis, S. egleis oweni, P. campestris, E. battoides, L. argyrognomon, P. saepiolus, E. amyntula, P. occidentalis, P. zelicaon, P. clodius, P. phoebus sternitzkyi, P. sonora.

Callahan, 15 VIII 80:

P. mylitta, S. saepium, L. melissa, P. acmon, C. philodice, P. occidentalis, A. campestris, P. communis.

Scott Mountain summit, 2 IX 80:

C. tullia eryngii, S. atlantis, O. sylvanoides, P. sabuleti.

Callahan, 2 IX 80:

P. mylitta, P. acmon (1 aberrant), *L. melissa.*

Mt. Eddy, 3 IX 80:

S. atlantis, S. egleis oweni, P. campestris, L. helloides, L. argyrognomon, L. melissa, P. saepiolus, E. amyntula, P. phoebus sternitzkyi, P. sabuleti.

Callahan - Gazelle Road, 6 IX 80:

C. sthenele silvestris, C. pegala boopis, C. tullia eryngii, P. mylitta, P. coenia, A. bredowii, L. melissa, C. philodice, C. eurytheme, P. beckerii, P. rapae, O. sylvanoides.

Callahan, 20 IX 80:

C. sthenele silvestris, C. tullia eryngii, S. zerene, P. mylitta, N. antiopa, V. annabella, V. cardui, P. coenia, A. bredowii, L. helloides, L. melissa, P. acmon, C. philodice, C. eurytheme, P. rapae, O. sylvanoides, A. campestris, H. juba, H. harpalus oregonia, H. columbia.

Gazelle Mountain (Callahan - Gazelle Road), 20 IX 80:

D. plexippus, C. sthenele silvestris, S. atlantis, S. zerene, P. mylitta, V. annabella, P. coenia, A. bredowii, L. arota, S. sylvinus, C. eurytheme, O. sylvanoides, H. juba, H. harpalus oregonia, H. columbia, P. sabuleti.

Gazelle, 20 IX 80:

D. plexippus, C. tullia eryngii, S. zerene, P. mylitta, P. satyrus, V. annabella, V. cardui, P. coenia, A. bredowii, L. helloides, S. melinus, L. melissa, P. acmon, C.

philodice, C. eurytheme, C. philodice X *C. eurytheme* hybrids, *P. occidentalis, P. rapae, O. sylvanoides, A. campestris, H. harpalus oregonia, P. sabuleti, P. communis.*

Weed, 20 IX 80:

D. plexippus, C. tullia eryngii, P. mylitta, P. zephyrus, N. californica, V. annabella, V. virginiensis, V. cardui, L. melissa, P. acmon, C. philodice, P. occidentalis, P. rapae, H. juba, P. sabuleti.

Mt. Eddy, 21 IX 80:

L. melissa, P. sabuleti.

Deadfall Meadow, 21 IX 80:

S. atlantis, S. zerene, P. zephyrus, N. milberti, P. mylitta, H. harpalus oregonia, P. sabulei.

Road 42N17 below Deadfall Meadow, 21 IX 80:

S. zerene, C. philodice, H. harpalus, H. columbia.

Scott Mountain summit, 21 IX 80:

C. tullia eryngii (common, fresh).

4.5 km E Gazelle, 4 X 80:

P. mylitta, P. coenia, L. melissa, C. philodice, C. eurytheme, P. rapae, O. sylvanoides, A. campestris, P. sabuleti, P. communis.

Mt. Eddy, 5 X 80:

S. egleis oweni, P. phoebus sternitzkyi (female).

Collectors: C. Kellner, M. Minno, D. Russell, A. M. Shapiro.

Appendix III

Notes on "The Butterflies and Some of the Moths of the Mt. Shasta Region," by F. X. Williams (1909)

This is the only faunistic paper to cover any place close to the Trinity-Eddy area. Williams penetrated the Trinity Divide and the Eddies, the Castella area, the McCloud River, and the headwaters of the Trinity River, but it is unclear just where. "Sisson" is the present Mount Shasta City. Williams gives a list of 87 species of butterflies. It should be remembered that this paper followed directly on the heels of W. G. Wright's *Butterflies of the West Coast*, filled with misdeterminations and taxonomic errors. Some of these are reflected in Williams' list. We here present his species list with equivalent modern names insofar as we have been able to determine them, and a few comments.

1. *Anosia plexippus* = *Danaus plexippus.*
2. *Argynnis leto* = *Speyeria cybele leto.* "Not uncommon at Sisson."
3. *Argynnis oweni* = *S. egleis oweni.*
4. *Argynnis zerene* = *S. zerene.*
5. *Argynnis monticola* = *S. hydaspe purpurascens.*
6. *Argynnis coronis* = *S. coronis.*
7. *Argynnis rupestris* = *S. callippe rupestris.* "In the valley."
8. *Argynnis epithore* = *Boloria epithore.*
9. *Melitaea chalcedon.* Identity uncertain. Reported as "very abundant in the valley... in June and early July." Wright's *chalcedona* is *chalcedona.*
10. *Melitaea palla* = *Chlosyne palla.*

11. *Melitaea hoffmani* = *C. hoffmanni segregata*.
12. *Melitaea leanira* = *C. leanira*.
13. *Phyciodes pratensis* = *P. campestris*.
14. *Phyciodes mylitta*.
15. *Grapta satyrus* = *Polygonia satyrus*.
16. *Grapta faunus* = *P. faunus rusticus*.
17. *Grapta zephyrus* = *P. zephyrus*. Apparently "rare" because no collecting was done late in the season.
18. *Vanessa antiopa* = *Nymphalis antiopa*.
19. *Vanessa californica* = *N. californica*. Records "swarming" in 1902, rare 1907.
20. *Pyrameis caryae (sic)* = *Vanessa annabella*.
21. *Pyrameis cardui* = *V. cardui*.
22. *Junonia coenia* = *Precis coenia*.
23. *Limenitis lorquini*.
24. *Heterochroa bredowii* = *Adelpha bredowii californica*.
25. *Coenonympha brenda* = *C. tullia eryngii* or *california*.
26. *Satyrus ariane* = *Cercyonis pegala ?boopis*.
27. *Satyrus silvestris* = *Cercyonis sthenele silvestris*.
28. *Chionobas nevadensis* = *Oeneis nevadensis*. Seen in 1902 but not in 1907 (i.e., even-year populations).
29. *Thecla grunus* = *Habrodais grunus*.
30. *Thecla halesus*. Apparently accurate, as a stray? (*Atlides*.)
31. *Thecla m-album*. Whatever this is, it could not be *m-album*; it may be a female *Mitoura spinetorum*.
32. *Thecla melinus* = *Strymon melinus*.
33. *Thecla californica* = *Satyrium*, but probably *sylvinus* since said to be "quite" plentiful along the stream margins."
34. *Thecla saepium* = *Satyrium saepium*.
35. *Thecla nelsoni* = *Mitoura nelsoni*.
36. *Thecla iroides* = *Incisalia iroides*.
37. *Thecla eryphon* = *Incisalia eryphon*.
38. *Thecla dumetorum* = *Callophrys*, species uncertain ("Canadian Zone").
39. *Chrysophanus virginiensis* = *Lycaena arota*.
40. *Chrysophanus gorgon* = *Lycaena gorgon*.
41. *Chrysophanus mariposa* = *Lycaena mariposa*.
42. *Chrysophanus zeroe* = *Lycaena nivalis*.
43. *Chrysophanus helloides* = *L. helloides*.
44. *Satyrium fuliginosa*.
45. *Lycaena heteronea*. Notes variability of females, some with blue.
46. *Lycaena fulla* = *Plebeius icarioides*.
47. *Lycaena saepiolus* = *Plebeius saepiolus*.
48. *Lycaena behrii* = *Glaucopsyche lygdamus behrii*.
49. *Lycaena sagittigera* = *Glaucopsyche piasus*.
50. *Lycaena podarce* = *Agriades glandon podarce*.
51. *Lycaena enoptes*. Uncertain; Wright's *enoptes* is *lupini*.
52. *Lycaena anna* = *Lycaeides argyrognomon anna*.
53. *Lycaena acmon* = *Plebeius acmon*, but perhaps including *lupini* which is common in the area.

54. *Lycaena piasus*, based on Wright's plate, is *Celastrina argiolus echo.*
55. *Lycaena comyntas* = status uncertain. Apparent *comyntas* occur at Dunsmuir.
56. *Lycaena amyntula = Everes amyntula.*
57. *Neophasia menapia.*
58. *Pieris sisymbrii.*
59. *Pieris occidentalis.* (*P. protodice* also occurs in exceptional years.)
60. *Anthocharis lanceolata.*
61. *Anthocharis creusa = Euchloe hyantis.*
62. *Anthocharis sara.*
63. *Colias eurytheme.*
64. *Colias chrysomelas = C. occidentalis chrysomelas.*
65. *Parnassius clodius.*
66. *Parnassius smintheus hermodur = P. phoebus sternitzkyi.*
67. *Papilio philenor = Battus philenor.* Stray from below Dunsmuir.
68. *Papilio zolicaon = P. zelicaon.*
69. *Papilio indra.*
70. *Papilio eurymedon.*
71. *Papilio rutulus.*
72. *Papilio daunus = P. multicaudatus.*
73. *Carterocephalus palaemon.*
74. *Pamphila juba* var. *viridis = Hesperia juba.*
75. *Pamphila comma = H. harpalus oregonia*?
76. *Pamphila agricola = Ochlodes agricola.*
77. *Pamphila pratincola = O. sylvanoides.*
78. *Pamphila siris = Polites sonora.*
79. *Pamphila vestris = Euphyes vestris.*
80. *Amblyscirtes vialis.*
81. *Pyrgus tessellata = P. communis.*
82. *Pyrgus caespitalis = P. ruralis.*
83. *Thanaos persius = Erynnis persius.*
84. *Thanaos propertius = E. propertius.*
85. *Eudamus pylades = Thorybes pylades.*
86. *Eudamus aemilea = Thorybes mexicana aemilia.*
87. *Eudamus tityrus = Epargyreus clarus.*

Williams describes the distributions of these species according to Merriam's life zones, but adds perceptively that "a difficulty which the entomologist is apt to encounter in tracing out the zonal ranges of certain insects, if his hunting grounds are in a mountainous country and he arrives there in midsummer or late summer, is that the insects which he sees at high altitudes and appearing peculiar to that level, may in late spring or early summer frequent the valley region as well." He found 76.3% of our Trinity-Eddy species in four seasons.

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Volume 18 *Number 1* *Spring, 1979(81)*

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Volume 18 *Number 2* *Summer, 1979(81)*

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Date of Publication: January 31, 1981

COVER ILLUSTRATION: Foxtail Pine (*Pinus balfouriana*) at tree line on Mount Eddy. This subalpine area is commonly used by hilltopping butterflies, while the much windier summit is not. (Phote taken 16 VIII 1979, by A. Shapiro.)

Volume 18 *Number 3* *Autumn, 1979(81)*

IN THIS ISSUE

Date of Publication: March 27, 1981

COVER ILLUSTRATION: Wing scales of *Hemileuca maia* viewed with scanning electron microscope (500X). C. LeMaire, pages 212-219.

Volume 18 *Number 4* *Winter, 1979(81)*

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Date of Publication: March 27, 1981

COVER ILLUSTRATION: *Danaus plexippus*, third instar larva, feeding on *Prestonia*. Young, pages 251-254.

INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

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Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

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Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

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IN THIS ISSUE

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COVER ILLUSTRATION: Foxtail Pine (*Pinus balfouriana*) at tree line on Mount Eddy. This subalpine area is commonly used by hilltopping butterflies, while the much windier summit is not. (Photo taken 16 VIII 1979, by A. Shapiro.)

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A Critique of the Genus *Boloria* (Nymphalidae) as Represented in "The Butterflies of North America", with Corrections, Additions and a Key to Species

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"The butterflies of North America" (Howe, 1975) has been criticized for a number of serious problems and errors (Belicek, 1976; Ferris, 1976; Leuschner, 1975; Orsack, 1975). Many of the generally unsatisfactory aspects are reflected in the treatment of the genus *Boloria* Moore, 1900, but there are a number of other errors that are not related to these features. It is the purpose of this paper to outline these errors and provide a basis for correcting them.

Although Howe should be commended for the quality of his illustrations (as paintings), many do not represent accurately the specimens of *Boloria*, either because of misrepresentation or transposition of plate captions. Part of this problem may be due to inaccurate reproduction of Howe's plates by the publisher. It is also unfortunate that size scales are not shown on the plates. This causes problems where size is a major distinctive character.

The author of the *Boloria* section (pages 243-252 in Howe, 1975) was Jon Shepard. He did not choose the specimens for representation, and was not asked to comment on the finished plates (Shepard, *in litt*).

Shepard also did not have an opportunity to review final page proofs, and much of his original manuscript was altered. It was first submitted in 1968, and a new one was submitted at a later date. Descriptions of species or subspecies appearing after 1968 were added by the reviewing editor, Dr. A. B. Klots. Some subspecies descriptions which appeared too late for inclusion are added herein.

Errors, Omissions, and their Corrections

1. Size of Figures.

It was mentioned earlier that size scales were not included with the plates. Presumably this is because *Boloria* figures were reported to be reproduced at actual size (Howe, 1975: 306, facing page). This is not correct. Plates of Lycaenidae were also produced at life size, but in comparing sections of these two groups of plates, our largest *Boloria* species appear little larger than many of the average sized Lycaenidae. It appears that some of the Lycaenidae are reproduced slightly larger and the *Boloria* slightly smaller than actual size.

2. Keys.

No key to the species of the genus *Boloria* was provided. Because a good key is almost indispensable to a collector who is unfamiliar with a group of species, I have constructed a simple key to the genus *Boloria* in North America. It is designed for field use without dissections or the use of visual aids, so certain diagnostic characters that are normally concealed from the eye are not used. The key is not sufficiently detailed to make possible identification of aberrant specimens, intergrades, or specimens at the extremes of normal variation in certain species.

The species of the genus *Boloria* are arranged in three subgenera: *Clossiana, Proclossiana,* and *Boloria.* Because the last two subgenera contain only one species each in North America, *B. eunomia* and *B. napaea* respectively, a key to subgenera is not provided.

The key was constructed from the study of specimens in my collection, and from original descriptions of the taxa in question.

Key to Adults of the Species of *Boloria* in North America

Abbreviations:
VFW - Ventral fore wing
VHW - Ventral hind wing
FW - Fore wing

1a. Submarginal spots of VFW whitish or silvered..... 2

b. Submarginal spots of VFW not whitish or silvered..... 12

2a(1a). Spots in postmedian-submarginal area of VHW open and silver or yellow centered..... *eunomia* (Esper, 1799)

b. Spots in postmedian-submarginal area of VHW closed, not silvered or yellow..... 3

3a(2b). Submarginal spots of VFW silvered or white (NOTE: some specimens of *B. selene tollandenis* have silvering reduced, but not absent)..... 4

b. Submarginal spots of VFW not silvered or white..... 6

4a(3a). Submarginal spots of VHW extended to and disrupting margin of wing..... 5

b. Submarginal spots of VHW not as above..... *selene* (Denis and Schiffermueller, 1775)

5a(4a). At least some submarginal spots of VHW capped by dark triangles with bases of some bent markedly basad (Fig.2)..... *freija* (Thunberg, 1791)

b. All submarginal spots of VHW capped by dark triangles with bases unbent, or only slightly bent basad (Fig. 3)..... *polaris* (Boisduval, 1828)

6a(3b). Submedian-median band of VHW continuous, solidly white, and bordered by heavy black..... *astarte* (Doubleday, 1847)

b. Submedian-median band of VHW broken or solid, but if solid, then tinted with yellow or brown..... 7

7a(6b). Portion of submedian-median band of VHW in discal cell silvered, the remainder unsilvered..... *napaea* (Hoffmansegg, 1804)

b. Not as above..... 8

8a(7b). Submedian-median band of VHW continuous and solidly yellow (in part; see note on page)..... *titania* (Esper, 1793)

b. Submedian-median band of VHW broken, or not solidly yellow 9

9a(8b). Submedian-median band of VHW clearly edged in black 10

b. Submedian-median band of VHW not edged in heavy black (see note on page)..... *chariclea* (Schneider, 1794)

10a(9a). Apical portion of VFW distinctly darker than rest of wing 11

b. Apical portion of VFW not distinctly darker than rest of wing ..... *distincta* (Gibson, 1920)

11a(10a). Postmedian band of VHW represented by a continuous band of white (in part)..... *freija* (Thunberg, 1791)

b. Postmedian band of VHW incomplete or if complete, only costal portion clearly white (in part; see note on page)..... *titania* (Esper, 1793)

12a(1b). Apical margin of FW angled; not smoothly curved (NOTE: some specimens of *B. bellona* from Alberta and British Columbia have this angle reduced and will key out to *frigga*. These can be distinguished from specimens of *frigga* by their brighter ground color on the VFW.)........ *bellona* (Fabricius, 1775)

b. Apical margin of FW evenly curved..... 13

13a(12b). Submedian-median band of VHW between Sc and Rs distinctly lighter than majority of remaining band..... 16

b. Submedian-median band of VHW uniformly colored..... 14

14a(13b). Submedian-median band of VHW in sharp contrast with rest of wing..... *kriemhild* (Strecker, 1878)

b. Submedian-median band of VHW not in sharp contrast with rest of wing..... 15

15a(14b). Black markings on VFW sharp and distinct (in part)........... *epithore* (Edwards, 1864)

b. Black markings on VFW weak and indistinct; rarely one or two sharp and distinct..... *alberta* (Edwards, 1890)

16a(13a). Markings on VFW weak; no distinct black spots.... *improba* (Butler, 1877)

b. Markings on VFW strong; Black spots distinct..... 17

17a(16b). Base of VHW at junction of Sc and R-M with silver spot (Fig. 4) ..... *frigga* (Thunberg, 1791)

b. Base of VHW at junction of Sc and R-M lacking silver spot (in part: NOTE: specimens of *frigga* from the Dempster Highway, Yukon, tend to have this spot reduced or lacking, and also lack the darker coloration of *frigga*. These can be separated from specimens of *epithore* by indistinct markings on the VFW..... *epithore* (Edwards, 1864)

NOTE: One of the major identification problems in this genus is distinguishing between *B. titania* and *B. chariclea*. These taxa intergrade in the Yukon and NWT, and Dr. C. D. Ferris has mentioned similar zones of possible intergradation in Alaska, northern Manitoba, and Labrador. Some specimens from Wyoming and Colorado, U.S.A., key out to *B. chariclea*. Before 1950 the forms now considered subspecies of *B. titania* were treated as forms of *B. chariclea*, or as separate species. Between 1950 and 1953 most of these subspecies were transferred to *B. titania* (Klots, 1951a, 1951b, 1953) without publication of the reasoning behind this decision. Recent work (Pike, in prep.) indicates that all North American subspecies are more similar to *B. chariclea* than to *B. titania*. It is outside the scope of this paper to present the reasons for this. For the sake of consistency with the presentation in Howe (1975), I follow Klots, bearing in mind that the Klots system is probably not the most accurate for presentation of the relationship between taxa.

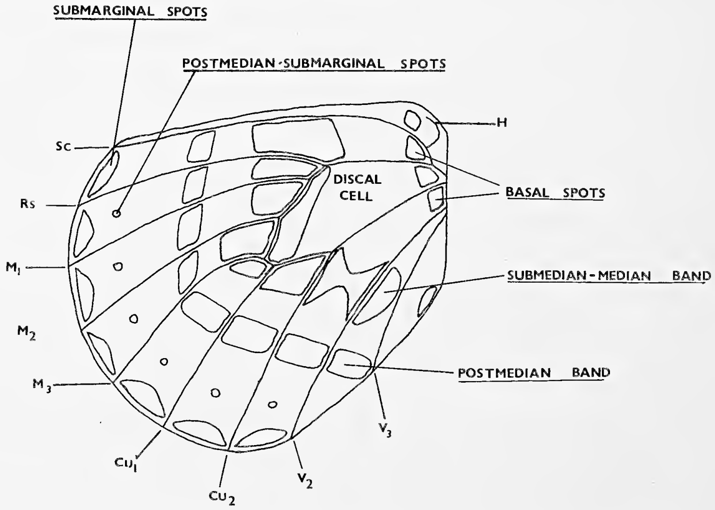


Fig. 1. Generalized hind wing of the genus *Boloria* showing important veins and markings on ventral surface: H, humeral vein; Sc, subcosta; Rs, radial sector; M, median; Cu, cubitus; V, vannus, or anal veins.

3. Author of the generic name *Boloria*

The generic name Boloria is credited to Reuss (Shephard, in Howe, 1975, page 243). In fact, it was proposed by Moore in 1900, the type species being *Papilio pales* Denis and Schiffermueller, 1775. In Europe it is restricted to the *pales-napaea-graeca* group of species, presumably first by Reuss, and later by Warren (1944).

4. *Boloria napaea reiffi* Reuss, 1925

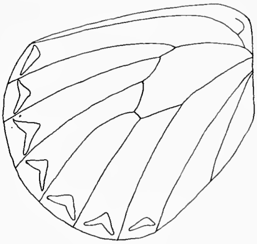
Shepard (in Howe, 1975, page 244) treats this form as consubspecific with *B. n. alaskensis* Holland, 1900. It was described as a species and has been the subject of controversy ever since. The type specimen is a male from British Columbia and has not been located. Klots (1940) treated this taxon as a subspecies and suggested it may be consubspecific with *B. n. alaskensis*. He had not seen the type but had located a specimen from Atlin, British Columbia, with characters resembling those of the description of *B. reiffi*. Warren (1944) also treated it as a subspecies, mentioned Klots' suggestion, and added one of his own; "The locality suggests that it might be a slightly abnormal specimen of subspecies *alaskensis*." He had not seen material of either *B. reiffi* or *B. n. alaskensis*. Dos Passos (1964) listed it as a subspecies as well. Shepard has synonymized the names *B. reiffi* and *B. n. alaskensis*, following the opinions of Klots and Warren. However, there is no justification for changing the status of *B. reiffi* now. A decision about its status must be based on study of the holotype or material that shares characteristics of this specimen. Possibly, such material is represented by unstudied specimens from colonies of *Boloria* near Fort Saint John, British Columbia, and north of Hinton, Alberta. Presumably it is considered a subspecies of *B. napaea* from characters given in the description and because of the lack of knowledge and specimens referable to this taxon.

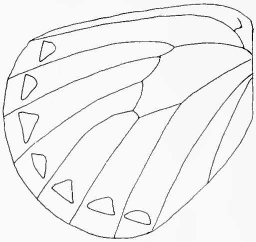
5. *Boloria eunomia* (Esper, 1799)

Shepard (in Howe, 1975, page 245) has misidentified *Boloria eunomia nichollae* (Barnes and Benjamin, 1926). There are two forms of *B. eunomia* found in the Rocky Mountains of Alberta and British Columbia; a light one and a dark one. Shepard has applied the name to the light form generally distributed in the Rocky Mountains, where, in fact, it should be restricted to the dark form found only in the vincinity of the Columbia Ice Fields, Alberta. From the original description, reproduced below, it is obvious that the specimen figured as *B. e. nichollae* (Howe, plate 34, Fig. 3) is not properly assigned.

"Upper side similar to dark specimens of *dawsoni*. Under side similar to *dawsoni* but darker, especially on the hind wing. We suspect this is a high altitude form."

Specimens of *B. e. nichollae* are stated by the authors to be darker on the underside than specimens of *B. e. dawsoni*. This is not true of the figured





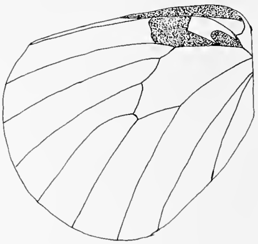


Fig. 2. Ventral Hind Wing of *Boloria freija* showing triangular caps on spots of submarginal band. Note the angled bases.

Fig. 3. Ventral Hind Wing of *Boloria polaris* showing triangular caps on spots of the submarginal band. Note the relatively straight bases.

Fig. 4. Ventral Hind Wing of *Boloria frigga* showing average extent of silvering in the area of the junction of Sc and R-M.

specimen. Ferris (1971) states that *B. e. nichollae* is a melanic high altitude form. The specimen figured is not melanic.

Shepard's justification for considering *B. e. nichollae* to be the light form generally distributed in the Canadian Rocky Mountains is that the collector, a Mrs. Nicholls, did not get closer to the Columbia Ice Fields than Laggan, Alberta, on her 1904 trip (Shepard, *in litt.*). Mrs. Nicholls (1905) published the itinerary of her trip, and from the dates and localities mentioned, she could not have visited the Ice Fields area. Subsequently, however, she collected specimens of *B. alberta* and *B. astarte* at the headwaters of the Saskatchewan and Athabasca rivers (Entomogical Society of Ontario, season summary page 118, 1907). These rivers emanate from the Columbia Ice Fields. At the same time, she probably collected the specimens that were eventually named *B. e. nichollae*. Examination of one male paratype from the USNM supports this hypothesis. Figure 5 illustrates the differences between *B. e. nichollae* and *B. e. dawsoni* from Alberta.

There has been some confusion about the type locality of *B. e. triclaris*. Shepard (page 245) states that the type locality is Labrador. Holland (1928) wrote that the type locality was "undoubtably Labrador". Barnes and Benjamin (1926) state that a short series of Labrador specimens is not similar in color pattern to specimens figured in Huebner's plates. Ferris

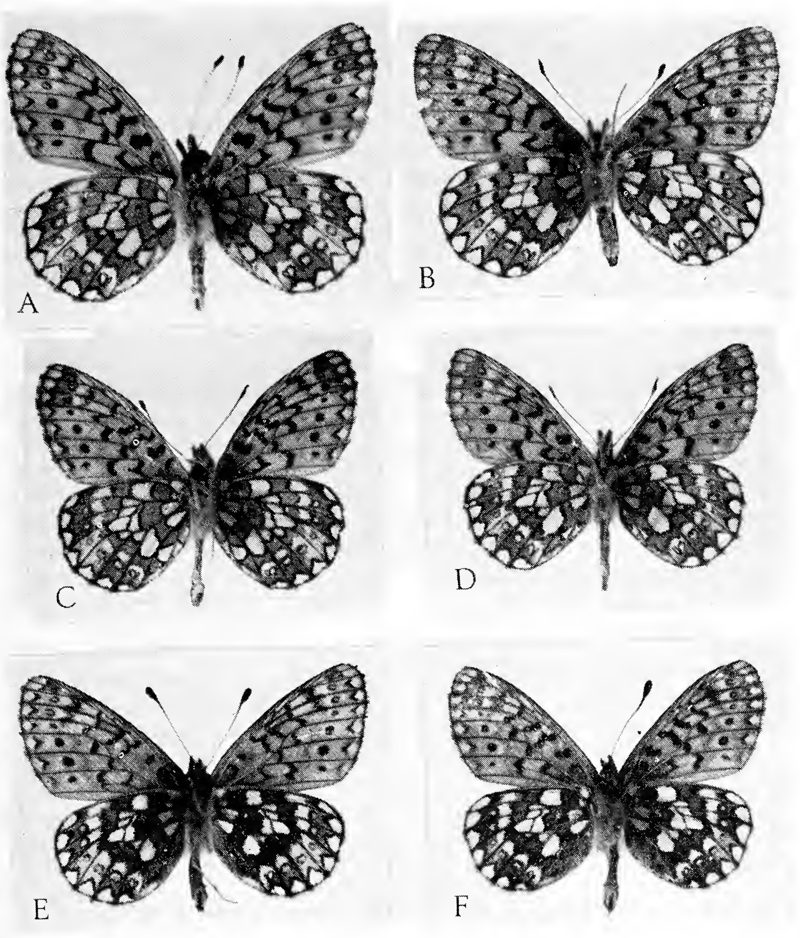


Fig. 5A. *Boloria eunomia dawsoni* male, Beaver Flats, Alberta, 18 VI 1971, Ted

Fig. 5B. *Boloria eunomia dawsoni* female, Plateau Mt., Alberta, 7500′, 26 VII 1975, Ted Pike

Fig. 5C. *Boloria eunomia dawsoni* male, 7 mi. E. Athabasca, Alberta, 16 VI 1974, Ted Pike

Fig. 5D. *Boloria eunomia dawsoni* male, 50 mi. W. Edmonton, Alberta, 18 VI 1976, Ted Pike

Fig. 5E. *Boloria eunomia nichollae* male, Wilcox Pass, Alberta, 7 VIII 1976, Ted Pike

Fig. 5F. *Boloria eunomia nichollae* male, Wilcox Pass, Alberta, 7 VIII 1976, Ted Pike

(1971) states the type locality is probably Labrador. In point of fact, Huebner fixed the type locality in his description of *B. e. triclaris* as Labrador, but the Labrador of 1821 was not the Labrador of today. Figures 6 and 7 show two official views of Labrador in the early 1800's, and much confusion existed at the time both officially and for the layman (Nicholson, 1954). Holland (1928) states that he had available specimens from eastern and western Labrador "that is, the eastern shore of Hudsons Bay." In view of this, I suggest that Huebner's concept of Labrador could have encompassed the whole of the Ungava Penninsula north of what was then Quebec. The problem is complicated by Huebner's figures. He shows one light specimen similar to specimens now considered *B. e. triclaris* and one dark specimen similar to material from Baker Lake, N.W.T., or to *B. e. nichollae*. Field (*in litt.*) and Klots (*in litt.*) have indicated that Huebner's material has been destroyed. Because *B. e. triclaris* has been considered the light form for over 150 years, I suggest it be retained as such. The type locality is hereby fixed as Nain, Labrador, Canada.

Unfortunately, characterization of the subspecies of *B. eunomia* is not complete (plate 245). *B. e. dawsoni, caelestis,* and *nichollae* are not described. Presumably we are to rely on the plates, but close examination shows that these do not fit the descriptions given. *B. e. denali* specimens are described as lightest in ground color, but the figures of *B. e. caelestis* (plate 35, Figs. 13 and 14) are lighter. *B. e. triclaris* specimens are supposed to be lighter than those of *B. e. dawsoni* on the upperside, but the figure (plate 34, Fig. 2) is much the same as those of *B. e. dawsoni* (plate 35, Figs. 16 and 17) with the latter having a lighter band on the hind wing. *B. e. laddi* specimens are stated to be unsilvered, this character to be used in separating them from, specimens of *B. e. caelestis*, but the figures of the latter are unsilvered (plate 34, Figs. 13 and 14). Specimens of *B. e. laddi* are not figured. All the subspecies should have been figured on the same plate for ease of comparison. In general, if the text is followed most of the subspecies can be distinguished from one another, but refer to Fig. 5 of this paper for *B. e. nichollae*. Specimens of *B. e. laddi* and *B. e. caelestis* are separated from one another by the darker subapical patch on the underside of the forewing, and the darker submarginal, median, and postbasal bands on the ventral forewing on *B. e. laddi* (Klots, 1940). *B. e. dawsoni* specimens are identified by their dark ground color, bright red bands and silvered markings on the ventral hind wing.

6. *Boloria selene* (Denis and Schiffermuller, 1775)

The name *B. selene albequina* is considered a junior synonym of *B. selene atrocostalis* (pate 246). Kohler (1977) revised this species, and retained *B. s. albequina* as a valid subspecies.

Here, again, the text and plates do not tally. *B. s. atrocostalis* is claimed to be intermediate between *B. s. myrina* and *B. s. terraenovae* in color and maculation (Shepard, in Howe, 1975, page 246) but the plates show *B. s. atrocostalis* (plate 34, Fig. 18) as the darkest of the three, with *B. s. terraenovae* (plate 34, Fig. 9) between it and *B. s. myrina* (plate 35, Fig. 1). Specimens of *B. s. nebraskensis* are distinguished from those of *B. s. myrina* by their larger size, but the figures are much the same and there are no scales to indicate size. Shepard states that six subspecies were described from North America but considers only five. Presumably *B. s. albequina* is to be the sixth, but what, then, of *B. s. marilandica* (Clark, 1941)? Both were subspecies described from North America, which makes a total of seven, two of which are not considered valid. Kohler (1977) has added an eighth subspecies, *B. s. sabulocollis*.

If the text is followed, the five subspecies are distinguishable from each other using the figure of *B. s. myrina* as a reference. *B. s. sabulocollis* is distingushed by its greater amount of yellow dusting on the VHW than *B. s. myrina*.

7. *Boloria bellona* (Fabricius, 1775)

The illustrations (plate 35, Figs. 4, 5 and 6) do not fit the descriptions in the text. *B. bellona toddi* specimens are stated to have the basal portion of the upperside of the wings dark, and specimens of *B. b. bellona* are stated to lack this darkening. Specimens of *B. b. jenistai* are said to have less darkening than *B. b. toddi* but more than specimens of *B. b. bellona* (page 247). The figures are much the same. Again the text is reliable.

8. *Boloria epithore* (Edwards, 1864)

Perkins and Perkins (1973) revised this species and treated four subspecies. The two new subspecies are *B. e. borealis* and *B. e. sierra*. Although there has been some controversy over the validity of these subspecies (Shepard, *in litt.*; Parshall, *in litt.*), until something is published refuting this work, these subspecies should be considered valid. Unfortunately, *B. e. borealis* is a junior homonym of *B. thore borealis* (Staudinger, 1861). Steps are being taken to correct this. The four subspecies can be distinguished as follows: *B. e. "borealis"* specimens have a greater degree of basal black dusting than *B. e. chermocki* and *B. e. epithore*, and they also have greyish marginal markings on the dorsal surface; specimens of *B. e. sierra* are distinguished by their greater degree of ferruginous coloring on the ventral surface.

9. *Boloria kriemhild* (Strecker, 1878)

Because adults of *B. kriemhild* and *B. epithore* are markedly similar in external features, illustrations of the two should appear on the same plate, for ease of comparison. Instead *B. epithore* is figured on plate 34, *B. kriemhild* on plate 33.

10. *Boloria frigga* (Thunberg, 1791)

Details in the description of *B. f. sagata* do not fit the specimen figured (plate 33, Fig. 4). Specimens are stated to have a lighter upperside than those of the other subspecies (plate 248), but on the plates they are the same. A series of 16 specimens from Colorado shows the upperside to be lighter than Alberta or Yukon material (excluding Dempster Highway, Yukon, material). Specimens of *B. f. saga* are supposed to have the basal area on the upperside suffused with black, but the plates show all subspecies with similar suffusion. The text is reliable.

The status of the Dempster Highway material is as yet unknown.

11. *Boloria titania* (Esper, 1793)

The six subspecies are not characterized in the text (pate 250). Rather than rely on the plates, I have prepared brief characterizations from the original descriptions. *B. t. boisduval* - median 0 submedian band not solidly white or yellow. Underside suffused with deep purple. Average

B. t. boisduvali - median 0 submedian band not solidly white or yellow. Underide suffused with deep purple. Average wingspan, 35 mm.

B. t. grandis - coloration as per *B. t. boisduvali.* Underside suffused with purple, and darker. Average wingspan, 40 mm.

B. t. montinus - median-submedian bank largely lacking white or yellow scaling. Underside without purple suffusion, tending to be more red. Less contrast on ventral hind wings.

B. t. rainieri - median-submedian band more yellow than preceeding subspecies. Much more contrast on hind wing underside than *B. t. montinus.*

B. t. helena - median-submedian band almost solidly yellow. No purple suffusion, tending to red-brown.

B. t. ingens - median-submedian band almost solidly yellow. Larger and darker than *B. t. helena.*

11. *Boloria alberta* (Edwards, 1890)

Shepard states that adults are present every year at Plateau Mt., Alberta (Shepard, in Howe, page 250). This is not quite true. It is true that they are not restricted to even-numbered years, but there are years in which no adults can be seen. It would seem, then, that adults are not present every year.

The type locality is Laggan, Alberta, the name of which was changed many years ago to Lake Louise Junction.

12. *Boloria astarte* (Doubleday, 1847)

Shepard considers *B. distincta* conspecific with *B. astarte* (Howe, 1975: 251). He also states that there is some controversy over this opinion. If this is so, it is best to leave *B. distincta* as the author described it, as a species, until its status is elucidated by study. The alternative is to change its status without adequate justification.

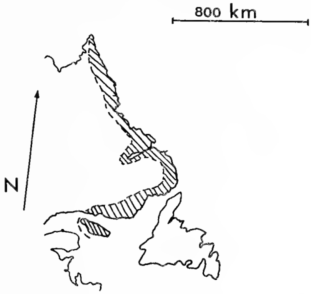


Fig. 6. Labrador according to the Hudsons Bay Company map by J. Arrowsmith published 1832. From "The Boundaries of Canada, its Provinces and Territories" by N. L. Nicholson.

Fig. 7. The limits of Labrador according to the Labrador act, 1809. From "The Boundaries of Canada, its Provinces and Territories" by N. L. Nicholson.

13. *Boloria polaris* (Boisduval, 1828)

If two subspecies are recognized, the figures (plate 34, Figs. 16 and 17) should be designated as one of these two subspecies and not simply *B. polaris*. Fortunately, adequate characterization is given in the text.

B. p. gorenlandica is omitted, presumably because it was described from Greenland, but specimens from Devon Island, N.W.T., agree with figures of *B. p. groenlandica*. If this subspecies is considered to be consubspecific with *B. p. polaris*, this should be mentioned in the text.

Discussion

In conclusion, the treatment of questionable or little known taxa is inconsistent. The name *B. reiffi* is relegated to synonymy, but the names *B. freija natazati* (Gibson, 1920) and *B. freija nabokovi* (Stallings and Turner, 1946) are considered valid, even though Shepard admits that he knows nothing more of these forms than is contained in the type descriptions, which is equal to his knowledge of *B. reiffi*. There is no discussion of taxonomic changes and no reference to original work in which these changes might have been published.

There is no discussion of where work is needed in this genus. In my opinion, the most important tasks in the future are:

1. Determination of the correct status of described forms in North America. Some of the previously described taxa were based on inadequately studied material, and I suspect that many do not represent valid taxa.
2. Elucidation of relationships, and construction of phylogenies, and reconstruction of biogeographies, with particular reference to relationships with European and Asian species.

In view of the large number of errors and inconsistencies in the treatment of this rather well known genus, I imagine that other genera will also be in a similar state. If so, I suggest that corrections to Howe's book be published or deposited in a central collecting area, perhaps with the publishers or with the editor. These could serve as the basis for a revised and corrected volume, should author and publisher care to issue a new edition.

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A Black-backed Larval Mutant of *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) in Japan

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Abstract. Six mutant larvae of *Lymantria dispar* (L.) were found in Sekigahara, Aichi Prefecture, Honshu, Japan, in June 1977. The distinctive 'black-backed' mutant late-stage larvae had nearly solid black dorsum. Otherwise, all setae, veruccae, and dorsal glands were colored as in normal larvae. All mutant larvae died of natural enemies, thus we could not determine if mutant larvae produced distinctive adults. The mutant appeared in less than 1% of the total population.

Introduction

The gypsy moth, *Lymantria dispar* (L.), is famous for variations in coloration among its different races or forms in both adults (Witt 1933, Mosbacher 1968) and larvae (Baltzer 1920, Monne 1927, Goldschmidt 1934). Recognizable mutants are also recorded. During 30 years of laboratory rearings, Klatt (1944) identified a larval mutant and two adult mutants. Frequencies of larval variants may occur as a result of differing ecological conditions and population densities, suggesting that different larval color variants have different adaptive advantages (Kolybin and Zelinskaya 1972). Herein we record further evidence of the genetic variability in coloration of *L. dispar* larvae.

In the Japanese archipelago, the gypsy moth has perhaps greater color variation than in any land mass of comparable size. Numerous publications by Goldschmidt, culminating in a review (1934), document variations in so-called 'sex-races' and variation in larval and adult coloration throughout Japan. Presently we report on the discovery of a rare larval mutant of the gypsy moth in central Honshu, Japan.

Description of Black-backed Larval Mutant

The mutant appeared perfectly normal in anatomy (Fig. 1A). The mature larval head capsule and body armature, including the dorsal (beta)

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veruccae (which are characteristically blue on the thorax and first two abdominal segments and brick red on the 3rd through 8th abdominal segments), setal armature, and dorsal glands, appeared normal. The striking characteristic of the mutant was the solid black background coloration of the dorsal integument on all thoracic and abdominal segments. Normally the dorsal integument is a mottled gray formed by intricate markings of black, white and varying degrees of yellow (Fig. 1B). The black of the mutant individuals extended laterally to a sharp demarcation line about 1 mm laterad of the dorsal veruccae (Fig. 1A). Laterally, the normal integumental coloration was present. In two individuals there was a slight yellow break in the solid black pattern at medial sites where yellow spotting often occurred in normal larvae. The individual illustrated (Fig. 1A) is one such exception while others were completely black and showed no yellow midline spotting.

Collection and Rearing of Mutants

The unusual mutation was found at Sekigahara, Aichi Prefecture, Honshu,Japan. Six mutant individuals were found between 4 and 21 June 1977 by the senior author. All larvae were on persimmon, *Diospyros kaki* Thunb., which was a common host for *L. dispar* larvae in south-central Honshu. *Lymantria dispar* caused recognizable levels of defoliation in individual trees or in small persimmon orchards during 1977. All *L. dispar* larvae found were scored in order to estimate the frequency of this mutation. Three mutants (n = ca. 250) were found on 4-5 June, 2 mutants (n = 109) on 19 June, and 1 mutant (n = 267) on 21 June. The mutant appeared in less than 1% of the population. By 21 June, widespread mortality from the fungus disease, *Entomophthora aulicae* (Reich.) Sorok. had depleted the populations although phenotypic scoring did include many dead or moribund larvae. The samples were made in different orchards but 5 of the mutant larvae were found in an area less than 300 meters squared. The 6th larva was found in an orchard located about 1.5 km from the first location.

Each of the 6 mutant larvae was isolated and reared on persimmon leaves. These mutants suffered from natural enemies as did the entire population. Of the 3 larvae collected on 4 June, 1 died from *Apanteles liparidis* Bouche and 1 from *Entomophthora aulicae*. The surviving larva pupated but was killed by emerging tachinid larvae, *Blepharipa* sp. The 2 larvae collected on 19 June died from *E. aulicae*. The final mutant larva pupated but was also killed by an emerging *Blepharipa* sp. larva.

One individual, killed by *A. liparidis*, has been preserved in alcohol, along with the parasite cocoons, and this specimen was deposited in the collection of the Division of Entomology, National Institute of Agricultural Sciences, Tokyo. The 2 diseased specimens collected 19 June were preserved dry but coloration differences from normal larvae did not

Fig. 1. Black-back mutant (A) and normal (B) last stage larvae of *Lymantria dispar* (L.) from Japan. Photos taken at Sekigahara, Aichi Prefecture, Honshu, on June 19-21, 1977.

preserve well. These two mutant specimens and a normal larva have been retained in the collection of the Asian Parasite Laboratory, USDA, Sapporo, Japan.

Discussion

Subsequent to our discovery of this mutant gypsy moth form in Japan, we learned of its presence in Korea. Dr. Hai-Poong Lee (Pers. comm. Oct. 1978) related that he and his students found ca. 20 black-backed specimens among nearly 200 larvae collected at Taejon, South Korea. What may reflect the more common occurrence of this mutant in Korea than in Japan, is the color illustration of a black-backed mutant individual in an Anonymous (1969, pg. 38) publication, in which the caption for the illustration does not mention the unusual coloration, suggesting that this condition may be common. Another illustration on the same page showed a dish containing at least 3 individuals with normal coloration. Both pictures were assumed to be of Korean specimens but this was not verified.

The presence of the black-backed mutant is not unique to the Orient. The same phenotype has been recorded in Europe (Klatt 1928, Baltzer 1920). According to Goldschmidt (1934), this phenotype was first found near Berlin by Klatt and was then found in other European localities by Baltzer, Kominsky, and Goldschmidt himself. Thus its presence in Europe has been well established. Although Goldschmidt studied the gypsy moth and traveled in Japan quite extensively, he never encountered this phenotype in the Orient to our knowledge. Our present record appears to be the first confirmation of this mutant in Japan. In Korea, its presence was documented by illustration but the author was apparently unaware that the illustrated larva was mutant; or did not consider it unusual or significant (Anonymous 1969).

It now appears that this mutant is more widespread than was previously thought. With its presence in Europe and the Orient established, we believe it probably has a Palearctic distribution.

Little can be concluded as to the success of this mutant in the Japanese population. No mutant larvae matured, thus it is unknown if any anomaly is expressed in the adult stage. Since the entire population suffered heavily from natural mortality, especially from the fungus disease, *E. aulicae*, it is very unlikely that many mutants contributed genetically to the subsequent generation. Further study in future seasons may again reveal the presence of this phenotype; thereby indicating a reoccurring expression of this mutation.

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Hibernal Diapause of North American Papilionoidea and Hesperioidea

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Abstract. Information from 695 sources (mainly scientific journals) is presented on the life history stage in which 348 species of butterflies and skippers spend the winter in North America. *Parnassius, Neophasia,* many Theclini (especially *Satyrium*), most *Lycaena*, and a few others diapause as eggs. Coliadinae, Satyrinae, most Nymphalidae, Riodininae, two *Lycaena* of Palearctic affinity, many Plebejini, and most Hesperiidae diapause as larvae. Most Papilionidae, Pierinae, many Theclini (especially *Callophrys*), many Polyommatini, and a few others diapause as pupae. *Danaus plexippus, Anaea andria, Nymphalis, Polygonia,* and some *Vanessa* diapause as adults. Records from Japan and Britain are very similar. The boreal or arctic-alpine species which have a two-year life cycle generally pass the first winter as a young larva, the second winter as a mature larva. The life history stage in which winter is passed significantly influences the time of flight of adult broods during the year.

Introduction

Insects in temperate climates must survive the cold temperatures of winter. To do this, insects have a phenomenon called hibernal diapause. Diapause is an arrested state of development. Growth and feeding of larvae stop, embryonic and pupal development cease, and mating and reproduction (egg development) of adults do not occur. Diapause is usually noticed when rearing is attempted; when the immatures reach a certain stage, they do not feed or develop further, and unless special precautions are taken, they will desiccate and die. The basic function of diapause is to allow insects to endure an unfavorable time such as a freezing winter. The tropical species which stray into temperate climates usually do not have diapause stages, and they soon die in temperate zone winters. The native temperate zone species, however, spend the winter in a diapause stage. Insects in general can spend the winter in any stage, including egg, larva, pupa, or adult, but a given species is usually adapted to diapause in only one stage. A few species may be able to winter in several stages, however. Some alpine and arctic species which have a two-year life cycle may winter in different stages during the two winters, as noted below. Good general discussions of diapause are by Chapman (2), Danilevskii (4), Beck (1), and Lees (14).

Physiological and sometimes morphological changes occur during diapause. Growth stops during diapause. During winter diapause insects increase the concentration of glycerol, sorbitol, or alcohol in their bodies, which acts as antifreeze to lower the temperature at which they freeze. Free water is converted to a colloid-bound state, preventing damage from freezing (4). Insects in diapause respire at a rate much less than normal (454), and they are quiescent and do not feed or grow. Diapausing larvae usually have one extra instar, which is usually specialized for winter survival (132, 459). The hibernating generation of *Asterocampa* has six instars, versus 5 for the summer generation, for example. *Chlosyne gorgone* and *nycteis* have a special diapause instar with russet colored larvae (529, 97). *Plebejus icarioides* larvae turn brown in the second instar when they diapause, and are green before and after that (535, 536). *Euphydryas editha* has a special diapause instar with a thicker integument (548).

Diapause of adult butterflies such as *Nymphalis* takes the form of an arrested state of development of their reproductive system; the abdominal fat in females is not converted to eggs until diapause is broken.

Two environmental factors, sunlight and temperature, regulate the appearance of diapause in most insects (1, 2, 4, 14). The number of hours of sunlight during the day (the photoperiod) has been found to be the critical factor in starting diapause in most insects. Diapause occurs only when photoperiod is below a critical amount. One stage in the life cycle is sensitive to photoperiod, which causes that stage or (usually) a later one to undergo diapause. Egg diapause is usually initiated by short photoperiod experienced by females laying the eggs, larval diapause by short photoperiod experienced by an earlier larval stage, pupal diapause by short photoperiod experienced by the larva, and adult diapause by short photoperiod experienced in larvae or (in ladybird beetles) the adult. For example, *Limenitis archippus* diapauses as larvae (306), *Papilio polyxenes* as pupae (305), and *Pieris napi* as pupae (377). In all three species, the long days of spring and early summer prevent diapause, but the short days of late summer and fall act on the larva to trigger diapause. In some insects high temperatures prevent the onset of diapause and low temperatures may bring on diapause. High temperatures prevent diapause in *Lycaena phlaeas* (334). In *Pieris rapae*, diapause never occurs at 24 degrees C, but at 20 degrees C, the photoperiod experienced by the fourth-instar larva influences the pupal diapause; with 10-hour days all the pupae diapause, but with 13-hour days none diapause (289).

In many species including *Limenitis archippus, Pieris rapae* and *P. napi* the photoperiod mechanism differs between geographic locations (306c, 1, 14); the critical photoperiod allowing continued development increases with latitude, because the diapause mechanism has adapted to the local sunlight conditions at each latitude.

Many species with only one brood per year have obligatory diapause; when a particular stage is reached, diapause occurs regardless of normal environmental conditions. Examples are *Papilio indra fordi, Anthocharis cethura* (535), *Euphydryas phaeton* (393a), and many *Satyrium*. Physiologically, this usually occurs because the critical photoperiod allowing development is greater than that found at the latitude of the habitat. Extreme laboratory conditions (constant light and warmth) sometimes can prevent diapause in these species (4). Ecologically, obligatory diapause is generally due to the absence of food plants or other necessities later in the season.

Generally, prolonged exposure to cold in the winter is necessary to "break" diapause and allow the insects to resume growing when the weather warms. Long days also break diapause in *P. polyxenes* (305). Diapause may terminate spontaneously merely due to the passage of time (40a).

The net effect of these mechanisms is that development usually starts when the weather warms in spring, and ceases when photoperiod triggers diapause (most multivoltine species), or when the diapause stage is reached (in the obligatory-diapause univoltine species).

This paper discusses only winter (hibernal) diapause, but summer (aestival) diapause sometimes occurs as well (328). The same cessation of development occurs in aestival diapause as in hibernal diapause, but it usually occurs during a time of year when droughts are frequent. Adult diapause is difficult to recognize; it is suspected when lifespan is unusually long and mating and reproduction do not occur, and dissections of females reveal fat body but no mature eggs. *Coenonympha tullia* adults (40) and *Euphydryas* larvae (509) may diapause in the summer in California which has a mediterranean climate. *Ochlodes sylvanoides* has a short mature larval diapause in early summer in California (535). *Agathymus* larvae may aestivate (12). *Speyeria* species have only one generation per year, but the flight period is very long (usually mid June to mid September), and diapause seems to occur during it. Edwards (5) and Scudder (21) found that *S. cybele, aphrodite,* and *idalia* females do not lay eggs until late August or September. Scudder found that *S. cybele* eggs do not become full size inside the female until mid August, and in Virginia adults are rarely seen in July (they are apparently diapausing). *Speyeria coronis* and *zerene* also have an adult diapause in summer (296a). The physiological factors producing aestival diapause are not as well known as those for hibernal diapause. In general long days and high temperatures cause aestival diapause. A geometrid moth *Abraxes miranda* has a short aestival diapause caused by long days and moderate temperatures (1). Low temperatures cannot play a large role in breaking aestival diapause, because summer is warm.

Results

This section presents the available data on hibernal diapause stage. The data are arranged in several tables. Table 1 contains the mostly temperate zone species which almost certainly have evolved a diapause stage. Table 2 contains the species which probably do not have a true diapause. These are semitropical species or species which may migrate into temperate regions each year. These species are often reported to spend the winter in several different stages; species without diapause continue to develop so that all stages can be present at a given time whenever the weather is mild enough not to kill them.

These data are based on 623 literature sources, on personal communications from 27 scientists, and on 46 of my own records. I searched all of the major entomology journals which have many papers on butterflies, and nearly all of the major works and papers on butterflies. Some references have undoubtedly been missed, but it is significant that the last several hundred references examined produced very few species-stage records not already found. Because slightly more than half of the approximately 700 species found in North America lack data on diapause stage, future contributions to the subject will come from rearing this unknown fraction and the species inadequately studied before now.

The data are cited by number (see Literature Cited). Authors of scientific names are not listed; they can be found in the references cited. The taxonomy of (427, 13, 12) is used except for recent changes that will appear in my forthcoming "Field Guide to North American Butterflies."

Discussion and Conclusions

Table 3 summarizes winter diapause information for nearctic species with adequate data, and compares it to Japanese (348) and British (11) information. Results are very similar among all three faunas. *Parnassius* usually diapause as eggs, but the remaining Papilionidae diapause as pupae. In the Pieridae, the Coliadinae usually diapause as larvae whereas the Pierinae usually diapause as pupae. Among the Nymphalidae, the Satyrinae and most other Nymphalidae almost always diapause as larvae, although *Anaea andria,* and the genera *Polygonia, Nymphalis, Aglais,* and some *Vanessa* (these four are closely related) diapause as adults. Among the Lycaenidae, the Theclini diapause as eggs usually, except for a large section (mainly *Callophrys*) that diapauses as pupae. Most American *Lycaena* diapause as eggs, but two American species (*phlaeas* and *cupreus*) belong to a Palaearctic group which diapauses as larvae. The Polyommatini usually diapause as larvae, occasionally as eggs or pupae. The Riodininae studied diapause as larvae. Hesperiidae usually diapause as larvae.

The larval diapause species are usually specialized to diapause as young, part-grown, or mature larvae. Most diapause as part-grown larvae, but a few (*Cercyonis, Speyeria,* and others) diapause as first instar larvae, and *Everes,* most Pyrginae, and several others diapause as mature larvae.

Several-year diapause of annual species. Occasionally species with life cycles of one year or less have longer life cycles because diapausing individuals do not emerge in spring but emerge only after another year or more in diapause. *Euphydryas chalcedona* larvae sometimes diapause for up to five years (54), and *E. editha* sometimes diapause for 2 years as larvae (138). Many pupal diapause species are known to do this (5, 385), including *Papilio aristodemus* (13, 377b), *P. cresphontes* (21, 95), *P. bairdii* (170), *P. zelicaon* (538, 315a, 335a), *P. polyxenes* (234, 101), *P. p. rudkini* (503, 477a, 22a, 427--six years), *P. indra* (412), *P. multicaudata* (167), *P. glaucus* (234), *P. g. rutulus* (167), *Eurytides marcellus* (234), *Anthocharis sara* (471, 167, 343a, 387a, 477a), *A. cethura* (471, 477a, 167, 535--five years), *A. lanceolata* (254, 477a, 421), *A. midea* (167, 234), *Euchloe ausonides* (167, 477a), *E. hyantis* (477a), *Pieris rapae* (482), and *Pieris sisymbri* (477a, 535--five years). Eggs might also diapause for several years. Several-year diapause would seem to be a useful adaptation to avoiding unfavorable years (290). Emergence of *Papilio aristodemus* (377b), *Anthocharis cethura* and *Euchloe hyantis* (535), seems to be stimulated by moisture in addition to cold. *Papilio polyxenes rudkini* and *Chlosyne neumoegeni* have summer and fall broods that seem to emerge from diapause as a response to rain; the more the rain, the larger the emergence (535).

Diapause stage of biennial species. Some boreal, arctic, and alpine species always have a two-year life cycle. They fly as adults only on alternate years, or at a given locality there are even-year and odd-year cohorts which rarely or never interbreed. Table 4 lists the species which are biennial, and summarizes the data on diapause stages from Table 1 for these species. For *Parnassius eversmanni* diapause occurs as an egg the first winter, then pupa the second winter, so that larval feeding occurs only on alternate years. For most other species, however, which include two *Colias, Chlosyne damoetas* (probably biennial), *Boloria alberta* ?, and seven *Oeneis,* the young larva spends the first winter, and the older or mature larva spends the next winter. This interpretation nicely explains the data on winter stages of *Oeneis,* which otherwise seem contradictory or confusing. Many other species of *Erebia, Boloria,* etc., are suspected of being biennial.

One very interesting aspect of biennialism is that when several biennial species occur together, they often fly on different years. For instance, *Oeneis chryxus* and *Neominois ridingsii* fly on Sonora Pass, Mono Co., California, at the same sites, *chryxus* in odd years, *ridingsii* in even years. *Oeneis jutta* and *O. chryxus* alternate years in Michigan, *O. jutta* and *O.* (*nevadensis*?) *macounii* alternate years in Minnesota. Adult interference during mate-locating behavior or larval competition may cause these species to fly in alternate years. Larval feeding in biennial species may be concentrated or restricted to alternate years. In eastern Alaska around Fairbanks, however, *O. jutta, O. polixenes, Erebia disa, Boloria astarte distincta, B. polaris, B.* (*titania*?) *chariclea,* and *Hesperia comma* all fly in odd-numbered years. In such cases perhaps the weather was so unfavorable in the past in an even-numbered year that all the adult cohort failed to mate and reproduce, and only the cohort occurring on the odd-years survived. Collectors returning from the far north often report such weather. Eventually, when more of the cohorts for biennial species have been discovered and mapped, a comparison with Pleistocene climatic events may help elucidate these patterns.

Non-diapause species. Contradictory information sometimes occurs for subtropical species which have no definite diapause stage (Table 2). Since these species develop during the winter, they may be found then in any stage. For instance, *Ascia monuste* develops year-around in Florida, and freezing winters kill the entire population (47). Some species such as *Euptoieta claudia* and *Precis coenia*, which have been reported to spend the winter in several stages, are warm-weather species which may actually have no diapause stage. Several species (*Colias eurytheme, Vanessa cardui*) may or may not have a true diapause. Hovanitz (525) and Shapiro (318) think that *eurytheme* may not have a true diapause, but the best data for this species indicate that it passes the cold winters in the larval stage as do its congeners with a true diapause. It has expanded its range northward within the last 100 years and may not have adapted yet to northern latitude photoperiods. Its close relative *C. philodice* has a similar pattern of winter stage records (Table 1). Williams (377a) states that *cardui* does not survive the U. S. winter in any stage, although many other authors (Table 1) give the adult as the most probable winter stage (as in other *Vanessa*), and Baker (304) thinks it may survive the British winter. *Danaus plexippus* diapauses as an adult, but mainly in Mexico and along the California coast (391, 426); it may not be able to tolerate temperatures far below freezing.

Ecological significance of hibernal diapause stage. The main benefit of a hibernal diapause stage is winter survival. Another significant feature is that the diapause stage is correlated with the seasonal appearance of the adults and other stages during the season. The adult diapause species fly first in spring, followed successively by pupal, mature larval, half-grown larval, young larval, and finally egg diapause species. The first instar diapause species often emerge as late in the season as the egg diapause species, because at least two of the egg diapause species (*H. comma, T. lineola*) actually diapause as first-instar larvae inside the egg. This seasonal progression is very striking among the univoltine species and among the first yearly brood of multivoltine species in Colorado (529, 536). It means that insect diapause strategies are adapted to the phenology of their host plants and habitats. The hibernal diapause stage may be adapted to the host plant in other ways. The egg diapause species commonly place their eggs on the larval host plant where the larvae will not need to search for food in spring. *Lycaena* usually diapause as eggs haphazardly placed around *Rumex* plants. The larval diapause species may or may not need to search for their host plants in spring, depending on where they diapause. The *Limenitis* (*Limenitis*) species diapause as larvae inside a cut-leaf case called a "hibernaculum," usually attached to the tree. *Speyeria* larvae sometimes diapause inside grass stems, and Melitaeini larvae commonly diapause under stones or logs. Many Pyrginae larvae diapause inside their silk tubes constructed from dicotyledon leaves, which fall to the ground in fall. The pupal and adult diapause species do need to search for the host plants in spring. The adult diapause species generally mate in early spring after spending the winter in crevices such as under bark (*Nymphalis, Polygonia*) or hanging from trees in dense aggregations (*D. plexippus*). It is conceivable that larval mortality may be high in spring for larvae which must relocate their host plants. The egg diapause species tend to have fewer broods than other species in Colorado; eggs may be better protected against desiccation than other diapause stages except pupae, so may be able to live longer.

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C. Personal records of J. Scott. Number 529. Most records are for Colorado; some are for California and elsewhere.

D. Records based on personal communication (numbers 530-554). 530 Richard A. Arnold, 531 Auburn E. Brower, 532 Lincoln P. Brower, 533 F. Martin Brown, 533a Robert P. Dana, 534 Scott L. Ellis, 535 John F. Emmel, 536 Marc Epstein, 537 Clifford D. Ferris, 538 Michael S. Fisher, 539 Jack L. Harry, 540 J. Richard Heitzman, 541 Roy O. Kendall, 542 Sterling O. Mattoon, 543 Lee D. Miller, 543a Douglas Mullins (pers. comm. to John F. Emmel), 544 Erval J. Newcomer, 545 Kilian Roever, 546 Arthur M. Shapiro, 547 Steven R. Sims, 548 Michael C. Singer, 549 Ray E. Stanford, 550 Fred T. Thorne, 551 David L. Wagner, 552 Ralph E. Wells, 553 Michael Young, 554 Steven Stone.

Table 1

Hibernal diapause stage for temperate zone species which probably have a true diapause. Diapause stage: E-egg, L-larva (instar given in arabic numbers, or y-young larva, h-part or about half grown larva, m-mature larva), P-pupa, A-adult. Diapause stage for biennial species is indicated by I-first winter, and II-second winter. e-probably an error; diapause probably occurs in the other stage listed for the species (some sources cited after an e may prove that diapause does not occur in this stage). r-winter rarely spent in this stage.

SPECIES	HIBERNAL DIAPAUSE STAGE	SOURCE
Papilionidae		
Parnassius phoebus	E-I	473, 449, 230, 5, 99, 131, 135, 536, 16, 529
	L (h, nearly m)-II	5, 536, 330a, 160a (L or P), 22a
Parnassius clodius	E-I	449, 99, 131, 135
	L (h or m)-II	535, 22a
Parnassius eversmanni	E-I	348
	P-II	348
Papilio glaucus	P	13, 9, 19, 20, 21, 540, 433, 5, 23, 58, 234, 431, 232, 234, 73, 62, 66
Papilio glaucus rutulus	P	532, 58, 546, 5, 15, 167
Papilio eurymedon	P	532
Papilio multicaudata	P	532, 272, 366, 5, 167, 251, 554
Papilio indra	P	427, 412, 310a, 374b
Papilio bairdii	P	5, 549, 170, 310a
Papilio polyxenes	P	13, 366, 20, 21, 23, 237, 540, 101, 220, 234, 275, 305, 15, 276, 433, 19, 8, 232, 234
	A(e)	21, 19
Papilio polyxenes rudkini	P	427, 503, 477a
Papilio polyxenes kahli	P	300
Papilio (polyxenes?) joanae	P	540
Papilio machaon	P	7, 52, 13, 227, 305
Papilio brevicauda	P	13, 23, 19, 129, 220
Papilio androgeus	P	310b
Papilio zelicaon	P	5, 538, 453, 305, 315a, 335a
Papilio cresphontes	P	19, 20, 21, 461, 23, 433, 540, 115, 113, 108, 232, 95, 104
Papilio aristodemus	P	13, 377b
Papilio xuthus	P	390
Papilio troilus	P	13, 366, 9, 540, 433, 23, 468, 19, 20, 21, 232, 66

Eurytides marcellus	P	13, 366, 19, 20, 21, 458, 252, 248, 246, 540, 81, 120, 5, 234, 8, 244, 433, 23, 457, 66, 234, 232, 65, 342a
Battus philenor	P	19, 433, 547, 13, 540, 519, 21, 23, 232, 276
	A(e?)	19, 13, 20, 21, 23
Battus polydamas	P	366, 384a
Pieridae		
Neophasia menapia	E	6, 427, 5, 15, 24, 58, 529
Anthocaris sara	P	427, 520, 471, 5, 167, 343a, 387a, 477a
Anthocaris midea	P	13, 19, 20, 540, 5, 15, 433, 23, 234, 144, 167, 241, 541
Anthocaris lanceolata	P	5, 421, 251, 254, 477a
Anthocaris cethura	P	167, 488, 477a
Anthocaris cethura pima	P	471
Euchloe ausonides	P	5, 529, 167, 327a, 477a
Euchloe olympia	P	13, 12, 540, 15, 245
Euchloe hyantis	P	427, 269, 488, 477a
Pieris napi	P	357a, 228, 13, 520, 3, 70, 129, 19, 20, 23, 431, 231, 365, 14, 4, 1, 377
Pieris rapae	P	191, 13, 433, 482, 289, 318, 540, 348, 23, 8, 15, 431, 374c, 331b, 19, 20, 21, 9, 67, 71, 303, 35, 289, 231, 232, 1, 328a
Pieris occidentalis	P	35, 527, 391a
Pieris protodice	P	13, 299, 318, 20, 19, 35, 23, 8, 21, 540, 433, 119, 71, 55, 31, 526, 232, 546, 391a
Pieris virginiensis	P	285, 13, 433, 12, 432, 413, 293, 348c
Pieris sisymbrii	P	477a, 535
Eurema nicippe	A	21, 20, 540, 519, 12, 299, 22, 278, 111, 19
	P?	232
Colias meadii	L(1)-I	162
	L(3-4, 5[r])-II	12, 226, 32, 5, 167, 147, 159
Colias scudderii	L(3-4)	226, 32, 5
Colias scudderii gigantea	L(y, 3)	12, 210
Colias palaeno	L(3)	12
Colias alexandra	L(2-4)	12, 226, 32, 5, 462, 384, 137, 147, 148
Colias (alexandra?) harfordii	L	5, 147
Colias interior	L(1, 2, 3)	13, 12, 222, 32, 185, 422f
Colias nastes	L(y, 3, m)-(I+II?)	13, 12

Colias eurytheme	L(3-4)	328a, 298, 482, 147, 433, 327, 318, 23, 21, 5, 546, 15, 19, 20
	P	482, 13, 299, 318, 5, 15, 232
	A(e)	482, 13, 299, 21, 15, 19, 20
Colias philodice	L(3-4)	19, 225, 13, 147, 166, 299, 433, 20, 525, 449, 21, 294, 32, 5, 15, 19, 439a, 38b
	P	13, 299, 48, 232
	A(e)	13
Colias hecla	L-I$^+$II	12, 13
	P?	13
Libytheidae		
Libytheana bachmanii	P	13, 225, 23
	A	15, 117, 19, 433, 232
Nymphalidae		
Coenonympha tullia	L(3-4, 5[r])	12, 434, 312, 424, 167, 140, 143, 145, 338a, 223a
C. tullia california	L(1)	338, 40
C. tullia heinemani	L(1?, 2, h?, m?)	434, 223a
Cercyonis pegala	L(1)	13, 299, 12, 21, 23, 5, 89, 106, 20, 132, 8, 536, 19, 15, 433, 540, 284, 423, 459, 516, 376, 380
Cercyonis meadii	L(1)	226, 12, 5, 376
Cercyonis oetus	L(1)	137, 376, 141, 226, 462, 12, 5
Cercyonis sthenele	L(1)	376, 12, 338a
Erebia magdalena	L(h)	529
Erebia theano	L(y)$^+$?-I&II	529
Erebia epipsodea	L(3-4)	12, 226, 229, 5, 529
Erebia discoidalis	L(4)	5
	P(e)	41, 286
Euptychia areolata	L(h)	225, 13, 5, 433, 19
Euptychia areolata mitchelli	L(4)	354, 12
Euptychia rubricata	L	515
Euptychia cymela	L(2[r], 4, m[r])	13, 299, 366, 423, 433, 225, 64, 20, 284, 21, 93, 23, 15, 8, 540, 19, 93, 429, 232
Cyllopsis gemma	L(4)	225, 366, 540, 5, 19, 232, 96, 130
Cyllopsis pertepida	L(h)	529
Oeneis alberta	L(m)?	502, 5
	P?	279
Oeneis uhleri	L(2, 3, 4, 5)	5, 12, 226
Oeneis melissa	L(y, 2, 3)-I	5, 469, 23, 225, 15, 19
	L(5)-II	5, 23, 225, 19
Oeneis polixenes	L(1, perhaps 2-3)-I	226, 12, 5
	L(4, 5)-II	5

Oeneis jutta	L(1, 2, 3)-I	19, 158, 12, 226, 225, 406, 5, 168
	L(4, 5, 6)-II	19, 155, 15, 225, 5, 168
Oeneis nevadensis	L(2, 3)-I	5, 176
	L(5)-II	5
Oeneis macounii	L(1, 2)-I	225, 5, 19
	L(m)-II	225, 5, 168
Oeneis chryxus	L(1, 2)-I	225, 45, 462
	L(3, 4, 5)-II	226, 12, 225, 45, 5, 462
Oeneis chryxus ivallda	L(h?)	5
Neominois ridingsii	L(2[r], 3-4)	5, 545, 462
Lethe portlandia	L	540
Lethe anthedon	L(3-4)	13, 299, 20, 540, 21, 123, 5, 8, 15, 23, 423, 433, 19, 232
Lethe eurydice	L(3-4, 5[r])	12, 13, 299, 474, 20, 22, 433, 21, 15, 5, 8, 19, 130, 144
Lethe appalachia	L(3-4)	481, 474, 295, 9, 540
Lethe creola	L	540
Danaus plexippus	A	19, 20, 21, 519, 8, 299a, 15, 228a, 391, 425, 426, 306a, 306b, 13, 477, 465, 433, 270, 157, 169, 36, 232, 83, 84, 116, 152
Anaea andria	A	13, 299, 402, 540, 277, 23, 276, 5, 273, 339, 340, 151, 332a, 260, 345, 19, 20, 232, 338b, 348d
Nymphalis antiopa	A	12, 427, 13, 284, 540, 236, 243, 529, 341, 342, 344, 345, 369, 276, 394, 235, 8, 215, 207, 21, 23, 177, 94, 87, 78, 303a, 448, 464, 5, 430, 58, 260, 519, 202, 190, 174, 169, 128, 157, 335, 238, 283, 287, 433, 467, 236, 19, 523, 332a, 304, 37, 71, 338b, 349a, 212, 393a
	P(e)	13, 19
Nymphalis milberti	A	427, 13, 337, 394, 369, 529, 433, 15, 283, 23, 62, 87, 78, 335, 332, 19, 177, 129, 169, 348b, 379a, 40b, 413a
	P(e?)	13, 15, 23, 19
Nymphalis californica	A	394, 335, 427, 12, 17, 529, 331b, 422d
	P(e)	17
Nymphalis vau-album	A	19, 21, 343, 23, 327, 15, 524, 433, 13, 299, 12, 156, 78, 87, 349a, 169, 8, 455, 430, 17, 58, 523, 519, 389a, 393a
	P(e)	17
Polygonia interrogationis	A	58, 23, 15, 540, 433, 340, 5, 19, 13, 20, 21, 9, 62, 78, 92, 232, 260, 186, 184, 183, 169, 161, 126, 144, 408a
	P?(e)	19

Polygonia comma	A	58, 519, 13, 299, 482, 340, 276, 346, 433, 9, 125, 78, 92, 5, 540, 23, 15, 260, 169, 262, 19, 20, 21, 37, 232
	P(e)	482
Polygonia progne	A	13, 20, 21, 340, 345, 8, 23, 430, 15, 433, 201, 105, 78, 169, 19, 37
	P(e)	19
Polygonia gracilis	A	19, 52, 212
Polygonia satyrus	A	225, 427, 394, 540, 342, 51, 215
Polygonia zephyrus	A	427, 51, 529, 297a, 331b
Polygonia oreas	A	529
Polygonia faunus (+ hylas)	A	349a, 13, 9, 396, 342, 433, 23, 58, 529, 19, 20, 21, 215, 51, 52
Vanessa atalanta	A	19, 396, 127, 304, 341, 169, 200, 520, 256, 284, 482, 433, 9, 23, 5, 15, 21, 540, 427, 12, 13, 327, 519, 536, 232
	P	19, 482, 9, 23, 15, 21, 540, 12, 13, 519, 348a
Vanessa carye	A	546, 536, 529, 393, 331b
	P	546
	L	546, 331, 520
Vanessa virginiensis	A	331b, 519, 12, 540, 169, 418, 433, 13, 299, 23, 21, 232, 482, 19, 536
	P	519, 12, 433, 13, 299, 23, 481, 15, 21, 482, 19
Vanessa cardui	A	232, 304, 299, 63, 78, 13, 274, 9, 20, 519, 433, 8, 23, 19, 21, 420, 344
	P	13, 423, 20, 519, 23, 19, 21
	L(e?)	331
Limenitis wiedemeyerii	L(3-4)	493, 5
Limenitis lorquini	L(2?, h)	427, 520, 338, 164
Limenitis archippus	L(1[r], 2[r], 3)	23, 13, 299, 21, 74, 103, 131, 455, 5, 8, 460, 459, 160, 232, 393b, 306c, 19, 146, 490, 482, 433, 20, 540, 472, 15, 306, 63, 144, 380a
	P(e)	144
Limenitis arthemis	L(2[r], 3, 4[r])	58, 15, 13, 433, 19, 472, 423, 20, 21, 23, 146, 8, 455, 5, 88, 103, 118, 380a, 393b
L. arthemis astyanax	L(2[r], 3)	13, 299, 540, 472, 23, 19, 20, 21, 121, 132, 430, 433, 393b
Limenitis bredowii	L	520
Asterocampa celtis	L(3-4)	8, 13, 12, 225, 299, 15, 69, 80, 131, 433, 23, 20, 540, 5, 19, 232
	E(e)	12
	A(e?)	225, 433, 20, 5

Asterocampa clyton	L(3-4)	13, 15, 20, 540, 433, 23, 112, 120, 131, 5, 19, 232
A. clyton subpallida	L(3)	516
Boloria titania	L(1, 4)(I&II?)	15, 529, 19, 160, 217, 12
Boloria epithore	L(4)	12
Boloria kriemhild	L(4)	12
Boloria selene	L(2-4)	544, 23, 15, 423, 20, 21, 13, 444, 433, 19, 80, 86, 132, 286a
	L(1)(e)	23, 291, 20, 21, 13, 444, 19, 80
Boloria alberta	L(1)-I	5
	L(h or m) or P-II	5
Boloria eunomia	L(3)	12, 160, 529
Boloria freija	L(4)	529, 160
	L(1)(e)	19
Boloria bellona	L(3-4)	225, 20, 21, 23, 433, 19, 80, 86, 132
	L(1)(e)	225, 13, 15, 21, 23, 19, 80
Speyeria nokomis	L(1, 3[r])	542, 534, 378
Speyeria idalia	L(1)	299, 21, 20, 540, 23, 86, 102, 433, 378
Speyeria cybele ($^+$ leto)	L(1)	299, 19, 20, 21, 540, 109, 75, 86, 5, 120, 132, 15, 180, 524, 23, 72, 12, 181, 397, 433, 37, 378
Speyeria diana	L(1)	9, 299, 540, 5, 23, 19, 72, 75, 86, 109, 120, 132, 378
Speyeria aphrodite	L(1)	19, 20, 21, 433, 109, 107, 23, 5, 423, 15, 413, 72, 75, 86, 378
Speyeria edwardsii	L(1)	12, 150, 378
Speyeria callippe	L(1)	12, 338, 5, 378, 338a
Speyeria atlantis	L(1)	12, 19, 20, 21, 15, 524, 5, 86, 149, 153, 378
Speyeria egleis	L(1)	5, 3, 100, 171, 378
Speyeria zerene	L(1)	44, 542, 378
Speyeria mormonia	L(1)	542, 378
Speyeria coronis	L(1)	137, 462, 542, 378, 338a
Speyeria adiaste	L(1)	542, 378
Speyeria hydaspe	L(1)	542, 378
Dymasia dymas	P(e?)	484
Phyciodes campestris	L(h)	546, 528, 393c
Phyciodes tharos	L(3)	13, 299, 427, 85, 90, 433, 225, 23, 423, 61, 15, 481, 296c, 5, 540, 8, 19, 20, 21, 452, 232, 393c
Phyciodes batesii	L(3)	13, 61, 209, 393c
Phyciodes mylitta	L(h-m)	546, 387
Phyciodes picta	L(2-4)	462, 98, 452, 137, 133
Phyciodes texana	L?	366
Chlosyne theona	L(4)	491, 411
Chlosyne chinatiensis	L(3)	539

Chlosyne leanira	L(3)	529, 427, 338a
Chlosyne leanira alma	L(3)	529
Chlosyne leanira fulvia	L(3)	529, 411
Chlosyne harrisii	L(3-4)	13, 223, 423, 20, 131, 191, 23, 137, 19, 523, 433, 15, 456, 61, 68, 90
Chlosyne nycteis	L(2[r], 3-4)	23, 529, 173, 433, 299, 13, 423, 20, 21, 349, 232, 49, 72, 79, 80, 90, 97, 15, 19
Chlosyne gorgone	L(2, 3, 4)	529, 330, 366, 213, 540, 213, 536, 173, 208
Chlosyne hoffmanni	L(h)	427, 358, 374
Chlosyne palla	L(h)	529, 323
Chlosyne damoetas	L(y)-I?	529
	L(3-4, 5?)-II	529
Chlosyne damoetas malcolmi	L (nearly m)	543a
Chlosyne neumoegeni	L(h)	427
Chlosyne gabbii	L(3)	50, 338a
Chlosyne californica	L(3)	550, 360
Chlosyne lacinia	L(3)	427, 172, 208, 377d
Poladryas minuta	L(3)	529, 541, 442
P. minuta arachne	L(3)	529
Euphydryas gillettii	L(4-5)	508
Euphydryas chalcedona	L(3[r]-4)	427, 529, 12, 450, 509, 251, 446, 24, 54, 134, 350b
E. chalcedona colon	L(h)	12
E. chalcedona anicia	L(h, 4, 5[r])	529, 167
Euphydryas editha	L(3[r]-4)	138, 154, 137, 427, 98, 439, 480, 462, 296, 98, 479, 5, 350a, 350b
	P(e)	24
Euphydryas phaeton	L(3-4)	13, 299, 327, 76, 79, 540, 90, 5, 134, 137, 15, 165, 462, 37, 393a, 463, 190, 191, 25, 433, 23, 282, 19, 20, 21, 417
Lycaenidae		
Apodemia mormo	L(m)	30, 427, 12, 324, 550
	E(e)	240
Apodemia nais	L(h)	529, 5
A. nais chisosensis	L(almost m)	28
Apodemia palmerii	L(3)	488. 427
Calephelis borealis	L(5-8 of 8-9)	13, 347, 12, 225, 433, 216
Calephelis muticum	L(4-5 of 8-9)	53, 12, 423, 15, 13
Caria ino	L(m)	28
Feniseca tarquinius	P?	19, 20, 21, 13, 142, 163, 433, 232, 481a
	A?	19, 20, 21, 13, 299
	L?	187, 163
Habrodais grunus	E	427, 497

Hypaurotis crysalus	E	353, 529, 34
Phaeostrymon alcestis	E	366, 12
Euristrymon favonius	E	12
E. favonius ontario	E	366, 422
Euristrymon polingi	E	361
Harkenclenus titus	E	13, 299, 12, 19, 20, 21, 15, 433, 466
Satyrium behrii	E	529, 427, 483
Satyrium saepium	E	529, 12, 492
Satyrium californica	E	12, 529
Satyrium tetra	E	427, 12, 500
Satyrium acadica	E	15, 23, 20, 433, 19
Satyrium auretorum	E	427, 12, 495
Satyrium sylvinus	E	12, 427, 319, 496
Satyrium calanus	E	13, 19, 21, 433, 23, 20, 225, 519
	L(1)(e)	15, 21, 23, 299, 519
	P(e)	122, 19
Satyrium edwardsii	E	20, 476, 13, 433, 15, 19
	L(1)(e)	476, 13, 15, 19
Satyrium liparops	E	12, 13, 19, 20, 423, 433, 15, 466, 23, 58
	L(y)(e)	23
Satyrium caryaevorus	E?	12
Satyrium fuliginosum	E	386, 529, 535
	L?	386
Atlides halesus	P	529, 400, 403, 232
Calycopis cecrops	P?	56
Strymon melinus	P	13, 12, 20, 540, 433, 466, 19, 21, 15, 518, 232
Erora laeta	P?	13, 19, 211
Panthiades m-album	P(e?)	13, 225, 357, 15, 19, 232
Callophrys eryphon	P	427, 352
Callophrys niphon	P	13, 19, 20, 15, 66, 197, 433
Callophrys lanoraieensis	P	523
Callophrys polios	P	13, 198, 433
Callophrys augustinus (+ *iroides)*	P	13, 423, 9, 20, 433, 19, 189, 194, 195
Callophrys mossii	P	552, 530, 529
Callophrys fotis	P	535
Callophrys irus	P	13, 19, 20, 433, 192, 193, 413, 33
Callophrys henrici	P	13, 225, 366, 540, 443, 8, 445, 196
Callophrys spinetorum	P	504
Callophrys gryneus	P	13, 423, 19, 20, 540, 23, 232, 433, 466
Callophrys gryneus nelsoni	P	427, 489
C. gryneus loki	P	427, 550
C. gryneus siva	P	268
Callophrys hesseli	P	57, 413b
Callophrys dumetorum	P	30, 379
	L(e)	471

C. dumetorum viridis	P	253, 379
Callophrys sheridanii	P	382
Callophrys macfarlandi	P	359, 280
Lycaena arota	E	529, 331, 3
Lycaena gorgon	E	427, 494, 470
	L(e)	494, 239
Lycaena helloides	E	529, 363, 546, 368
	L(e)	387
	P(e)	387, 267
Lycaena hyllus	E	13, 20, 437, 15, 19, 433, 529, 203, 60
Lycaena xanthoides	E	427, 500
L. xanthoides editha	E	529
L. xanthoides dione	E	540, 529
Lycaena hermes	E	427, 498, 336, 308
Lycaena epixanthe	E	13, 12, 225, 20, 19, 433, 413, 199, 60, 199
Lycaena dorcas	E	206, 203, 29, 221
Lycaena nivalis	E	544, 310
Lycaena mariposa	E	368
Lycaena heteronea	E	427, 551, 529, 46
Lycaena rubidus	E	551, 529
Lycaena cupreus	L(h)	203. 535
Lycaena phlaeas	L(y, 2-3; m?)	348, 7, 26, 169, 19, 20, 21, 437, 334, 59
	P(e?)	433, 19, 20, 21, 437, 15, 23, 225, 13
Plebejus argyrognomon	E	348, 188, 400
Plebejus melissa	L(h; m?)	43, 19
	P?	19
Plebejus icarioides	L(2)	12, 427, 331, 536, 497, 530, 281, 355, 205
	P(r)	205
Plebejus saepiolus	L(1, h)	12, 13, 427, 513, 214
	P(e?)	438
Plebejus acmon	L(2-3)	333, 382, 383
Plebejus lupini	L(2)	333
Plebejus neurona	L(2)	333
Plebejus emigdionis	L(late larva)	427, 489
Plebejus optilete	L	12
Everes amyntula	L(m)	427, 500, 258, 19, 451
Everes comyntas	L(m)	12, 13, 423, 257, 20, 15, 433, 21, 19
	P(e)	232
Agriades glandon	L or P	529
Brephidium exilis	P	266, 381
Glaucopsyche lygdamus xerces	P	250, 261, 514, 375
Glaucopsyche lygdamus	P	427, 13, 423, 255, 250, 375
	L(m)(e)	19

Glaucopsyche piasus	P	427, 265
Celastrina argiolus	P	13, 529, 433, 22, 5, 447, 19, 20, 21, 77, 82, 91, 137, 144
	L(e)	433, 144
Celastrina nigra (= ebenina)	P	392
Philotiella speciosa	P	427, 489
Euphilotes rita	P	529
Euphilotes enoptes	P	226, 441
Euphilotes battoides	P	494, 415, 427
Hesperiidae		
Zestusa dorus	P	435
Autochton cellus	P	13
Epargyreus clarus	P	13, 299, 370, 423, 9, 519, 8, 259, 433, 15, 23, 529, 19, 20, 21, 232, 66, 124, 182, 251
Pyrgus communis	L(m)	512, 19, 433, 13, 423
	P(e?)	19, 299, 20, 13, 423
Staphylus hayhurstii	L(3)	309, 322
Pholisora catullus	L(m)	13, 299, 370, 423, 433, 23, 519, 15, 19, 20, 139
	P(r)	9
Erynnis lucilius	L(m)	299, 19, 20, 433
Erynnis persius	L(m)	19, 20, 21, 23, 419, 433
Erynnis baptisiae	L(m)	433
Erynnis brizo	L(m)	9, 19, 20, 21, 66, 433
Erynnis icelus	L(m)	299, 19, 438(h), 18, 136, 433, 20, 21
	P(e)	136
Erynnis juvenalis	L(m)	299, 19, 20, 21, 438h, 372, 9, 23, 66, 522, 519
	P(e)	232
Erynnis zarucco	L	13, 362
Erynnis horatius	L	370
Erynnis tristis	L	488
Erynnis martialis	L(m)	433, 19
Gesta gesta	L(m)	370, 478
Celotes nessus	L	370
Celotes limpia	L	541, 475
Systasea pulverulenta	L(m)	367, 370
Cogia outis	L(m)	370
Cogia caicus	L(m)	27
Thorybes valeriana (= mysie)	L	545
Thorybes pylades	L(m)	492, 499, 427, 433, 178, 370
	P(e)	19, 20, 21, 13
Thorybes bathyllus	L(m)	370, 19, 433
	P(e)	19, 13, 423
Achalarus lyciades	L	370
	P(e)	19, 299, 13

Thymelicus lineola	E	225, 292, 223b, 436, 376a
Copaeodes aurantiaca	P?	370
Carterocephalus palaemon	L(m?)	19, 348
Oarisma garita	L(4)	204
Oarisma powesheik	L(5 or 7)	325
Ancyloxypha numitor	L(3-4)	505, 433, 437, 19, 219, 20, 21, 373, 232
	P(e?)	505, 299, 437, 19, 20, 21
Hesperia leonardus	L(1-2)	19, 219, 249, 20, 13, 423, 433
Hesperia leonardus pawnee	L(1)	529, 533a
Hesperia leonardus montana	L(1)	529
Hesperia dacotae	L(5)	533a
Hesperia pahaska	L	521, 427
Hesperia ottoe	L(5)	351, 401
Hesperia metea	L(m)	321, 9, 540, 327
	P(e?)	13, 249, 19
Hesperia columbia	L?	521
Hesperia comma	E	521, 388, 405, 406, 407, 408, 409, 179
Hesperia lindseyi	E	521, 427, 12
Hesperia juba	E or L(1-3)	521
Hesperia nevada	L or P	521
Hesperia miriamae	E?	521
Hesperia sassacus	P?	20, 21, 13, 433, 19
Hesperia viridis	L?	370
Euphyes bimacula	L(h)	529
	P?	19
Euphyes dion	L(3)	540
Euphyes vestris	L(3)	314, 540
Pompeius verna	L?	13, 219
	P?	219
Poanes zabulon	L(m)?	19, 20, 21
	P?	19, 20, 21
Poanes viator	L or P	373
Poanes hobomok	E, L, P?	437, 225, 15, 249, 218, 242, 433
Polites sabuleti	P	317
Polites mardon	P	317
Polites themistocles	P	225, 13, 511, 23, 19, 20, 21, 433, 218
	L?	218
Polites coras	L(1-5)	433, 506, 13, 299, 20, 21, 19
	P	506, 433, 13, 299, 20, 21, 19
Polites origines	L(3-4)	13, 510, 19, 218
	P?	19
Polites mystic	L(4)	226, 423, 507, 19, 21, 20, 13, 433
Ochlodes sylvanoides	L(1)	331, 427
	E?	427
Paratrytone melane	L?	486

Problema byssus	L(4)	371, 12, 540
Atrytone logan	L?	13, 423, 19
	P?	13, 423
Atrytone arogos	L(4 of 6)	327, 540, 481
Panoquina panoquinoides errans	L	485
Wallengrenia egeremet	L(h)	13, 423, 433, 19, 218, 249
Amblyscirtes hegon	L(1)	399
	P?	19
Amblyscirtes celia belli	L(4)	316
Amblyscirtes nysa	L(h-m)	315, 540
Amblyscirtes aenus	L(h)	529
A. aenus linda	L	540
Amblyscirtes vialis	L	540
	P(e)	19, 13, 423, 23
Atrytonopsis hianna	L(m)	329, 540
Megathymus yuccae	L(h-m)	12, 495, 39, 25, 326, 517, 25b, 25c
Megathymus ursus	L(3, 4, 5)	12, 25b
M. ursus violae	L(h)	529
Megathymus cofaqui	L	263
M. cofaqui harrisi	L	9
Megathymus streckeri texanus	L	271
Megathymus streckeri streckeri	L	26a
Stallingsia smithi maculosus	L	350
Agathymus neumoegeni	L(1-3)	311, 38
Agathymus polingi	L(1-3)	311
Agathymus evansi	L(1-3)	311
Agathymus aryxna	L(1-3)	311, 12
A. aryxna baueri	L(1-3)	311
A. aryxna freemani	L(1-3)	311
Agathymus alliae	L(1-3)	311, 12
Agathymus mariae	L	313, 224

Table 2

Species which probably have no diapause stage. These are mainly subtropical species or migrants to temperate areas. For explanation of symbols see Table 1. n-source states that no diapause occurs.

SPECIES	WINTER STAGE	SOURCE
Papilio palamedes	P	13, 23, 366(n), 19, 114
	L	13, 23
Nathalis iole	A	540, 296b(n)
	P	233
Phoebis sennae	A	15, 23, 21, 20, 19
	P?	232
	L?	21, 20, 19
Phoebis agarithe	L(y)	297
Eurema lisa	A	15(n), 23, 12, 13, 482(n), 20, 19(n)
	P	12, 13, 232
Colias cesonia	A	327(n), 273, 404, 277, 540
	P	13, 427, 232, 363a, 370a(n)
Ascia monuste	L, P, A	302, 47(n)
Euptychia hermes	L	320, 366(n), 13, 232
Agraulis vanillae	L, P, A	332a(n), 395(n), 288(n), 232, 364a, 260a(n), 370a(n)
Euptoieta claudia	A	23, 423, 540, 21, 13, 225, 12, 20, 19, 232, 277
	P	23, 540, 21, 20, 19
	L	23, 8, 21, 20, 19, 16, 277
Precis coenia	A	232, 482, 23, 13, 12, 540, 433, 327(n), 520(n), 19, 20, 21
	P?	546, 387
	L	546, 529, 387
Calephelis nemesis	L or P	487
Ministrymon leda	P?	501
Strymon columella	L?	498
Panoquina ocola	L or P	364
Nyctelius nyctelius	L	301
Lerodea eufala	L, P?	264
Polites vibex	L or P	370
Atalopedes campestris	A?	13
Lerema accius	P?	13, 19
Perichares philetes	L	301
Calpodes ethlius	L or P	370, 482(n), 260a(n)
Urbanus proteus	A	225, 19
Heliopetes macaira	?	370(n)
Heliopetes laviana	L	370
Phocides polybius	L	356
Cogia calchas	L	372

Timochares ruptifasciatus	L	389
Cabares potrillo	L	389
Xenophanes trixus	L	389
Chioides catillus	L	372, 370
Staphylus mazans	L or P	370
Chiomara asychis	?	389(n)

Table 3

Hibernal diapause stage of Nearctic, Japanese, and British butterflies (E-egg, L-larva, P-pupa, A-adult).

	Nearctic				Japan				Britain			
	E	L	P	A	E	L	P	A	E	L	P	A
1. Papilionidae												
Parnassius	3	2	1		3		1					
other Papilionidae			17				13				1	
2. Pieridae												
Coliadinae		10		1		2	1	4		2	1	1
Pierinae	1		13			3	5				3	
3. Lycaenidae												
Theclini	17		21		25	1	2	3	4		1	
Miletini						1						
Curetini								1				
Lycaenini	12	2				1				2		
Polyommatini	1	10	10		4	8	4		2	9	1	
Riodininae		6									1	
4. Nymphalidae												
Polygonia, Nymphalis, Aglais, Vanessa				12				10				6
Anaea				1								
Danainae				1								
Satyrinae		27				18	1	1		10		
other Nymphalidae		52	1		2	23	3	1	1	8		
5. Hesperiidae	3	59	7		2	13	2		2	5	1	
Total	37	168	70	15	36	70	32	20	9	36	9	7

Table 4

Biennial species: hibernal diapause stage, cohort of adult flight (even or odd years), and documentation of biennialism. Diapause stages from Table 1.

SPECIES	HIBERNAL DIAPAUSE STAGE	ADULT FLIGHT TIME & LOCATION	DOCUMENTATION FOR BIENNIALISM
Parnassius eversmanni	E-I P-II	Japan	348
Parnassius phoebus, clodius	E-I, L-II	-----	-----
Colias meadii	L(1)-I L(3-4, 5 [r])-II	Alberta	162
Colias nastes	L(y,3,m)-(I+II?) P?	-----	-----
Colias hecla	L(I+II), P?	-----	12, 13
Chlosyne damoetas	L(y)-I? L(3-4, 5?)-II	every yr. Colo.	529
Boloria alberta	L(1)-I L(h or m) or P-II	mostly even yrs. Alberta, mostly odd yrs. Plateau Mtn. Alberta	5, 200, 247, 529, 398a 414b, 12
Boloria astarte	-----	even yrs. Washington, even and odd yrs. Alberta	414b, 12, 17, 529, 398a
B. astarte distincta	-----	mostly even yrs. in north, mostly odd yrs. in south	*, 370b
Boloria polaris	-----	odd yrs. central Alaska, Manitoba, mostly even yrs. rest of range	*, 385, 329a, 393d, 422c, 414c, 331a
B. (titania?) chariclea	L(1,4) (*titania*)	odd yrs. Alaska, Yukon	*, 370b
Oeneis jutta	L(1, 2, 3)-I L(4, 5, 6)-II	odd yrs. Alaska, Michigan, Wisconsin, Minnesota, Saskatchewan; even yrs. Colo., Manitoba, Newfoundland, Ontario, New Brunswick, Maine, Labrador, Quebec	385, 42, 168, 25a, 419a, 417a, 398b, 414c, 529, 10, *, 377c, 422c, 422a, 414a, 329a, 331a
Oeneis polixenes	L(1, perhaps 2-3)-I L(4, 5)-II	odd yrs. Alaska; even yrs. Maine	*, 351a, 422c

Oeneis melissa	L(y, 2, 3)-I L(5)-II	every yr. Colo.	167, 5, 19
Oeneis uhleri	L(2, 3, 4, 5)(I+II?)	biennial Alberta; may be more common odd yrs. Colo.	5, 529
Oeneis nevadensis	L(2,3)-I L(5)-II	even yrs. Wash., Vancouver Island; mostly even yrs. Oregon & Sonoma Co. Calif.	395a, 5, 369, 17, 385, 398, 332, 422e, 12, 344a, 300
Oeneis (nevadensis?) macounii	L(1, 2)-I L(m)-II	odd yrs. Alberta, Saskatchewan, Riding Mts. Manitoba; even yrs. eastern Manitoba, Ontario, Minnesota	167, 385, 10, 374a, 422a, 398c, 168, 175, 375a
Oeneis chryxus	L(1, 2)-I L(3,4,5)-II	even yrs. Michigan & so. Colo., odd yrs. Sonora Pass Calif.; mostly odd rest of Calif. (*ivallda*)	385, 529, 307, 416, 422e
Oeneis taygete	-----	odd- & even-yr. cohorts differ in phenotype in N. Wyoming; even yrs. Labrador	385, 537, 414c, 543, 414
Oeneis alberta	-----	biennial Colorado?	553
Neominois ridingsii	L(2[r], 3-4)+?	even yrs. Sonora Pass Calif.	529
Erebia disa	-----	odd yrs. Alaska, Saskatchewan; even yrs. part of Saskatchewan	*, 385, 10, 318a, 422c
Erebia theano	L(y)+?-I&II	even yrs. throughout Colo.	385, 529
Hesperia comma	*E* + ?	odd yrs. Alaska; even yrs. Churchill Manitoba	*, 329a
Pyrgus centaureae	-----	mostly odd yrs. Colo.	529

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*references 405, 406, 407, 408, 409

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Description and Taxonomic Implications of an Unusual Arizona Population of *Apodemia mormo* (Riodinidae)

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Abstract. *Apodemia mormo* in the region of Nogales, Santa Cruz Co. Arizona, display variability unusual even in the *A. mormo* complex. At least five overlapping phenotype classes, some represented elsewhere by relatively uniform populations, are present in the area. The relationship of these specimens to adjacent *mormo* is unclear. It is possible that a "population" such as this may represent two or more entities isolated by such factors as voltinism and foodplant choice; larger samples and breeding experiments will be required to investigate this.

Southwestern populations of *Apodemia mormo* (Felder & Felder) display a complex variation pattern rivalled by few Nearctic butterflies. The only comprehensive treatment of the species to date is that of Opler & Powell (1961), and nearly 20 years later adequate population samples are lacking from many areas, especially northwestern Mexico. Samples at hand provide a somewhat confusing and contradictory picture. In some areas, there is evidence of latitudinal or altitudinal clines in the orange to black wing patterns, yet the reverse seems to occur elsewhere. Other difficulties include ill-defined intergradation zones, polytopy involving widely separated phenotypes, and voltinism differences between nearby demes. Powell (*in litt*) suggests the possibility of temporally isolated sibling species in some areas, and Emmel & Emmel (1973) feel some California populations may represent sympatric entities kept distinct by use of different *Eriogonum* larval foodplants. Langston (1974), in discussing voltinism in Caliornia *mormo*, questions the conspecificity of *A. m. mormo* and *m.virgulti*. With the occurrence of such distinct and restricted races as *A. m. langei* Comstock and *A. m. duryi* (Edw.), our understanding of this group is obviously far from complete.

In microcosm, the complexities involved with *A. mormo* are displayed by samples from Santa Cruz Co., Arizona, in the vicinity of Pena Blanca Lake and the Atascosa Mountains, northwest of Nogales (see Fig. 1). Here, the habitat consists of rolling oak-grass savanna, as characterized by Lowe (1964), at *ca.* 4200′ (1280 m) elevation. *A. mormo* is widespread but uncommon, and is often captured singly at blooms of *Baccharis glutinosa*

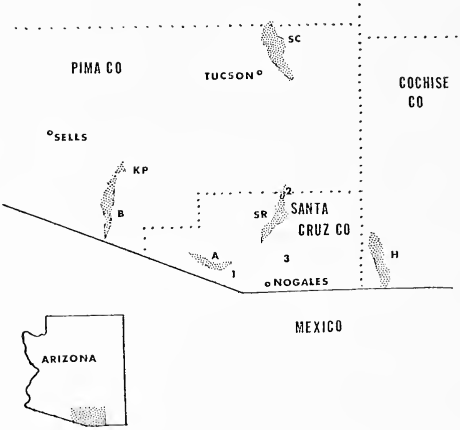

Fig. 1. Southern Arizona locales for *Apodemia mormo* discussed in text. A: Atascosa Mts., B: Baboquivari Mts., H: Huachuca Mts., KP: Kitt Peak, Quinlan Mts., SC: Santa Catalina Mts., SR: Santa Rita Mts. 1: Pena Blanca Lake, 2: Box Canyon, Santa Rita Mts., 3: Sonoita Creek. Approximate scale: 1 inch = 25 miles (1 cm = 18 km). Inset: region of Arizona covered by Fig. 1.

Pers., *Aloysia*, and other flowers. *Eriogonum wrightii* Torr., a common southeastern Arizona foodplant for *mormo*, is not abundant in the area; no specimens known to the author were found directly associated with it. Three specimens were collected by the author at flowers of another *Eriogonum* (possibly *E. abertianum* Torr.). The populations appear to be at least trivoltine (III-V, VII-VIII, IX-X), in contrast to bivoltine (IV-V, VIII-IX) sequences at the north bases of Kitt Peak and the Santa Rita Mts., and the east side of the Huachuca Mts.

Arizona *mormo* populations lacking DHW orange are currently referred to *m. mormo*. Those with orange scaling on the DHW (and often VHW) are referred to *m. mejicana* Auct. (Behr?). As observed by Opler & Powell (1961), neither of these "subspecies" is itself homogenous; *mejicana* is highly variable *within* populations as well.

Examination of 20 *mormo* (12 ♂♂, 8 ♀♀) from the Pena Blanca Lake area revealed the following (see appendix):

1. The sample is extremely heterogenous, even for *mormo* (Fig. 2). At least five overlapping phenotype classes are present: two specimens

resemble the subspecies *maxima* (Weeks) both in size (the ♀ to 20 mm FW length) and color pattern; five large females (to 21 mm FWL) are of a dark *mejicana* phenotype, with variable DHW orange; two specimens fit the popular concept of *mejicana* (i.e. Huachuca Mts.); a fourth category is characterized by greatly reduced orange dorsally and increased white scaling along the subterminal DHW band. An Oslar record of *m. mormo* from Nogales is cited by Opler & Powell (1961); such a phenotype would result from further reduction of orange in these specimens. The fifth class forms a variable intermediate group having considerable DFW orange and extenstive white scaling along the subterminal band. One male of this group was found associated with the "large" *mejicana* females (group two). The extreme variation prevented exact assignment of each individual to one group or another.

2. It is noteworthy that none of the above categories is *restricted* to the Nogales region, but each occurs in varying frequencies elsewhere, sometimes as a relatively uniform population. For example, the large *mejicana* specimens (Fig. 2, row 3, *a*) are quite similar to scattered individuals from the Baboquivari Mts., Sonoita Creek, and the Box Canyon area of the Santa Rita Mts. (see Fig. 1). They also show affinities with specimens from far to the east (Davis Mts., Texas). The Sonoita Creek and Baboquivari Mts. populations given evidence of trivoltinism as well. Powell (*in litt*) notes the similarity between August specimen from the Chiricahua Mts. (near Portal) and the fourth phenotype discussed above. Specimens from near Douglas (Perilla Mts.) are also of this type.

The trivoltine "large" *mejicana* phenotype is not present in large samples from low elevation orange VHW populations at Kitt Peak, the Santa Rita Mts., and the Huachuca Mts. The darker phenotypes in the Nogales sample are equally separable from dark higher altitude specimens from Kitt Peak and the Santa Ritas (Fig. 2, row 3, *b* and *c*), especially with respect to the white scaling along the subterminal DHW orange band (as in *m. mormo*, Fig. 2, row 4, *b*).

The similarity of occasional individuals from Nogales and the Santa Catalina Mts. to *maxima* is intriguing. Although no uniform populations of this phenotype are known from north of central Baja California, it may apparently be produced in both juniper-oak and low desert habitats.

Superficial observations on "similarities" are not meant to neglect genetic implications. As indicated by Mayr (1963), very similar phenotypes may be produced by different gene assortments in sympatric populations. Mayr also observes that color patterns may not be correlated with maximum adaptibility, but may be the result of pleiotropic effects of genes controlling phenotype survival. In this regard, care must be taken in assessing the relationship of the Pena Blanca *mormo* with nearby populations.

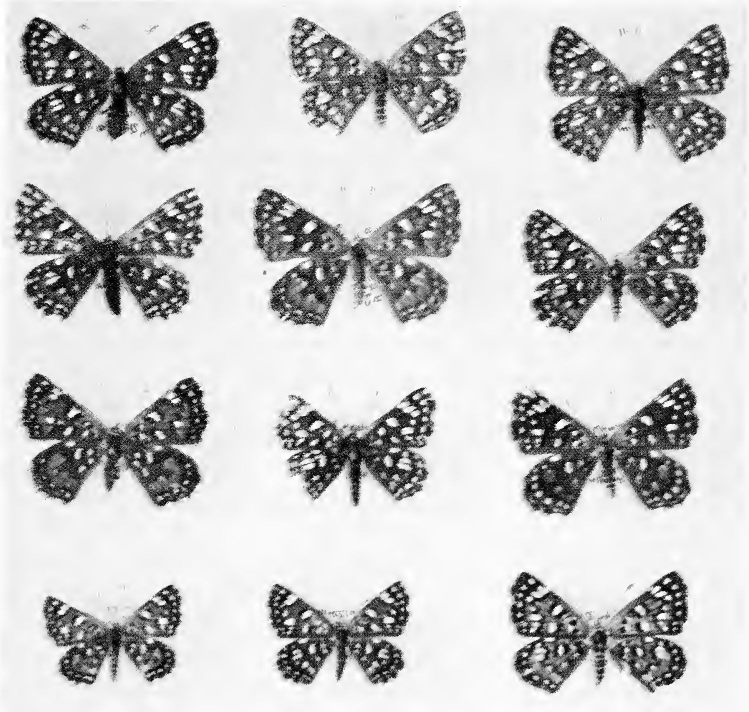

Fig. 2. *Apodemia mormo* (dorsal) from Arizona and Baja California.

Row 1. *A. m. maxima* ♀, Loreto, Baja Calif. Sur, 1 Dec. 1977, GSF. "Maxima" phenotype ♀, Molino Canyon, 4200′, Santa Catalina Mts., Pima Co., Ariz., 23 Oct. 1960, Wm. Hedges. "Maxima" phenotype ♀, Summit Motorway, Atascosa Mts., Santa Cruz Co., Ariz., 24 Feb. 1978, R. Bailowitz.

Row 2. "Mejicana" phenotypes: Box Canyon, 4700′, Santa Rita Mts., Pima Co., Ariz., 11 Aug. 1978, GSF (♀). Ruby Road, Atascosa Mts., Santa Cruz Co., Ariz., 9 Aug. 1977, J. W. Brown (♀). Elkhorn Ranch, Baboquivari Mts., Pima Co., Ariz., 20 Mar. 1978, GSF (♀).

Row 3. Dark "mejicana" phenotypes: Summit Motorway, 4500′, Atascosa Mts., Santa Cruz Co., Ariz., 4 Aug. 1978, GSF (♀). Tres Amigas Cyn., Atascosa Mts., Santa Cruz Co., Ariz., 18 Mar. 1978, R. Bailowitz (♂). Kitt Pk. Road, 4200′, Quinlan Mts., Pima Co., Ariz., 11 Sept. 1974, GSF (♀).

Row 4. Light "mejicana" phenotype, 2 mi. W. of Pena Blanca Lake, Santa Cruz Co., Ariz., 31 July 1979, RAB (♀). "Mormo mormo" phenotype, N. Base Kitt Peak, 3800′, Quinlan Mts., Pima Co., Ariz., 29 April 1977, GSF (♂). Light "mejicana" phenotype, N. Base Kitt Pk., 3800′, Quinlan Mts., Pima Co. Ariz., 1 Oct. 1974, GSF (♂).

A "blend zone" concept, as postulated by Opler & Powell (1961) for (primarily) California intergrade zones, does not seem to account for all variation observed in southern Arizona:

1. There is little evidence that gene flow (at present) is appreciable in this area, where *mormo* populations are often discrete and restricted to montane and foothill associations. As the species tends not to occur in the

creosote bush-mesquite scrub between mountain ranges, it is difficult to document interbreeding of races. However, Bowden (1979) observes the importance of historical ecological factors in influencing wing pattern phenotypes observed today; conceivably populations that are presently sympatric were not even discrete during more favorable climatic periods.

2. Variation in *mormo* involves an altitudinal component which must be carefully considered. How, if at all, does a montane population relate to those from 3000′ below? Such altitudinal differences tend to produce allochronic populations even in the same mountain range.

3. With the isolated populations, the character and size of the blend zones are difficult to assess. Very similar variation patterns are present in the Baboquivari Mts. and Davis Mts., Texas, yet the latter are remote from any *m. mormo* influence. And although a striking intergrade zone exists at Kitt Peak, Tilden (*in litt*) records both *mormo* and *mejicana* at Sells, almost 20 miles (32 km) northwest. Is the blend zone width defined by these records, or are they samples from distinct populations?

4. Occasional phenotypes are found that normally occur in distant populations. Richard Bailowitz records a single specimen of the dark *mormo* phenotype from Onion Saddle at *ca.* 8000′ (2440 m) in the Chiricahua Mts., well southeast of the normal range of *m. mormo*. A further example is the occasional presence of the *maxima* phenotype in southern Arizona.

5. In at least one case, contiguous races have not developed an appreciable intergrade zone. At the western edge of the Colorado Desert in California, *A. m. virgulti* (Behr) and *A. m. deserti* Barnes & McDunnough are evidently parapatric in the transition zone from foothills to desert. Evidence for intergradation is slight; approximately 50 m separate the races at Mountain Springs Grade in San Diego Co., yet in a sample of 40 specimens only three suggest intergradation, and these may represent variation in *virgulti*. Opler & Powell (1961) cite intermediate phenotypes from Riverside Co., but these lack precise locale data. This California zone admittedly differs from the Kitt Peak intergrade zone (a steeper topological gradient and restriction of each form to a different *Eriogonum*) but the orange-banded vs gray-white phenotypes involved are similar in the DHW color patterns.

It is evident that the 9-11 accepted subspecies of *mormo* are of limited value in handling variation of this magnitude. Nevertheless, it is instructive to note the occurrrence of a named race in widely separated areas. A striking example is the presence of *A. m. dialeuca* Opler & Powell in the mountains of both California and Baja California Norte (Stanford, 1973). Such polytopic races, the often abrupt phenotypic changes with altitude, and discrete populations, suggest multiple factors control the phenotypic plasticity observed in Arizona.

In the region between Sells and the Santa Rita Mts. (including Nogales), it seems probable that transitional and localized selective pressures have not effectively channeled the color patterns in a single direction. Polymorphic intergrade populations would then result from intermediacy in the selection factors which elsewhere produce more uniform phenotypes. The resulting demes would be further subject to altitudinal modification; phenotypic reversion to "mormo" well within a zone occupied by "mejicana" would then be explicable. In the broad transition from *mormo* in the low western deserts to *mejicana* in the southeastern desert grassland, intermediacy in environmental factors often parallels intermediacy in phenotypes; the Nogales populations show evidence of altitudinal effects as well.

The *mormo* complex shows a phenotype composition resulting from the interaction of poorly understood climatic, topographic, and biotic selection factors. The heterogenous population described here shows that a relatively uniform phenotype in one area (such as *maxima*) is in another only one component of a highly polymorphic assemblage. Understanding of variation in the Nogales region, based on further collecting and breeding experiments, would certainly help determine relationships in this difficult group.

Acknowledgements: I thank Richard Bailowitz, Nogales, John W. Brown, San Diego Natural History Museum, Dr. F. H. Rindge, American Museum of Natural History, and Dr. J. W. Tilden, San Jose, for information and/or loan of specimens. I am also grateful to David Kennedy, El Paso, for the photography, and to Dr. Jerry A. Powell, University of California, Berkeley, and Dr. James R. Zimmerman, New Mexico State University, for comments on the manuscript.

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Appendix

Data from Specimens Examined, Grouped by Phenotype Classes

Conclusions on seasonal and sexual variation in the Nogales area are limited by the small sample size, dates of capture in seven months, and samples from scattered locales. Collectors: Richard A. Bailowitz (RAB), John W. Brown (JWB), and Gregory S. Forbes (GSF).

ARIZONA: Santa Cruz Co.:

Group 1.: *maxima* phenotype. Ruby Rd., *ca.* 5 mi W Pena Blanca L., 4400′, 9-VII-1977 (JWB), 1 ♂. Summit Motorway, Ruby Rd., 4 mi W Pena Blanca L., 4300′, 24-III-1978 (RAB), 1 ♂.

Group 2.: "dark" *mejicana* phenotype. Ruby Rd., 3.5 mi W Pena Blanca L., 4200′, 12-VIII-1975 (GSF), 1 ♀. Ruby Rd., 0.7 mi W Summit Motorway, 4400′, 4-VIII-1978 (GSF), 2 ♀♀. Ruby Rd., *ca.* 5 mi W Pena Blanca L., 4400′, 9-VIII-1977 (JWB), 2 ♀♀.

Group 3.: "light" *mejicana* phenotype. Ruby Rd., 2 mi W Pena Blanca L., 400′, 31-VII-1979 (RAB), 1 ♀. Ephraim Cyn., 1 mi W Nogales, 3900′, 20-IX-1978 (RAB), 1 ♂.

Group 4.: reduced orange with white subterminal band scaling. NW side, Pena Blanca L., 3900′, 23-III-1978 (RAB), 1 ♀. Tres Amigas Cyn., Atascosa Mts., 18-III-1978 (RAB), 1 ♂. Summit Motorway, Ruby Rd., 26-III-1978 (GSF), 1 ♂. Alamo Cyn., Atascosa Mts., 30-III-1978 (RAB), 1 ♂.

Group 5.: "intermediate" *mejicana* with white subterminal band scaling (not illustrated). 4 mi W Pena Blanca L., 7-VIII-1979 (GSF), 1 ♂, 11-VIII-1978 (RAB), 1 ♂. Ruby Rd., 0.7 mi W Summit Motorway, 4-VIII-1978 (GSF), 1 ♂. Ruby Rd., *ca.* 5 mi W Pena Blanca L., 9-VIII-1977 (JWB), 1 ♂. Potrero Cyn., 7 mi W Nogales, 23-X-1977 (RAB), 1 ♂. Tres Amigas Cyn., 3 mi S Ruby, 13-V-1979 (RAB), 1 ♂. 0.8 mi W Pena Blanca L., 4000′, 21-VIII-1975 (GSF), 1 ♂.

* * *

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Chromosome Studies Including a Report of B-Chromosome in a Wild Silkmoth, *Sonthonnaxia maenas* (Doubleday) (Saturniidae:Saturniinae)

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Abstract. The diploid chromosome number in *Sonthonnaxia maenas* (Doubleday), a wild silkmoth from India, is 62 and is being reported for the first time. The mitotic and meiotic interphases in female show a prominent, positively heteropycnotic body (sex chromatin). Besides a B-chromosome has also been discovered in two individuals and its behaviour during mitosis and meiosis has been described.

Introduction

The genus *Sonthonnaxia watson* comes under the group of tailed silkmoths of the tribe Saturniini, with two other genera, *Actias* and *Proactias* (see Arora and Gupta, 1979). *S. maenas* forms a papery, open, pale-gold-colored cocoon, the silk of which has not been commercially exploited. It is distributed in northeastern India extending into Bhutan, China and Burma, etc. (Arora and Gupta *loc. cit.).*

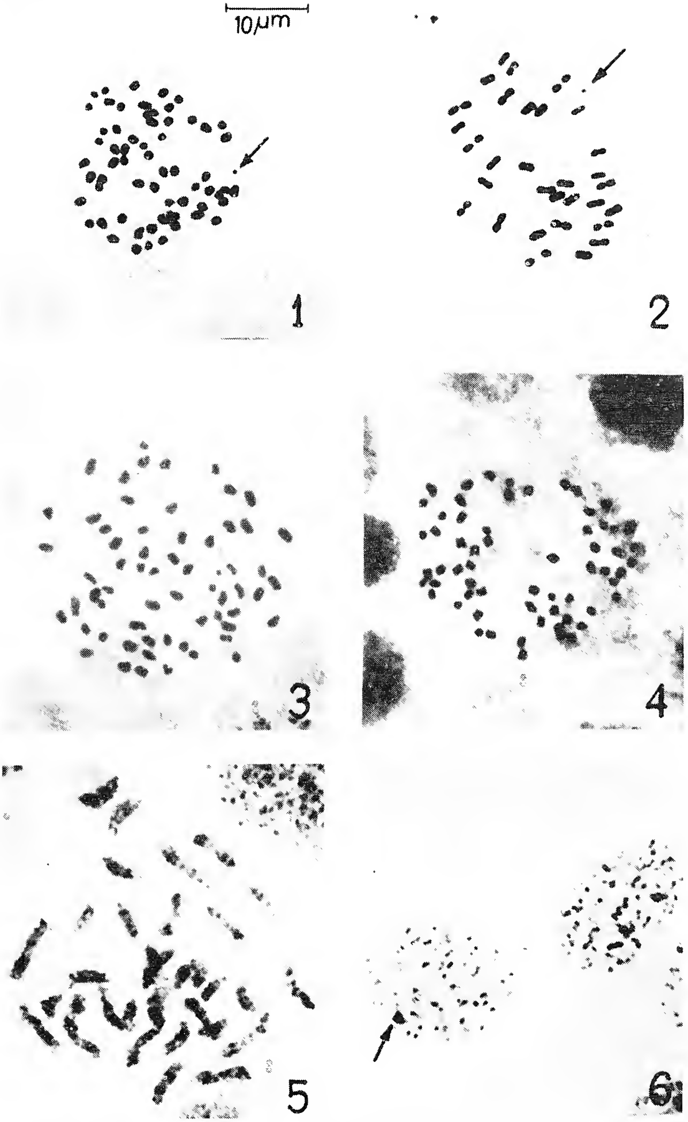
The present paper, which forms the first report in the genus *Sonthonnaxia* for chromosome cytology, includes studies on chromosome complement, sex chromatin, meiotic mechanism and B-chromosome in both the sexes.

Material and Methods

The cocoons used in this study were collected during October-November, 1979 from Khasi Hills, Meghalaya, at an altitude of about 4000 feet. The chromosome preparations were made from 2 ♂♂ and 1 ♀ pupae by heat-dried suspension method described earlier (Narang and Gupta, 1979a). However, before staining in 2-5% Giemsa buffered at pH 6.8, the slides were dipped in glacial acetic acid for 30 seconds to reduce the cytoplasmic staining. Some cocoons were also kept for emergence for taxonomic purposes.

Observations

The diploid chromosome number in both the sexes is invariably 62 as studied at metaphases in 36 cells including 12 spermatogonial (Fig. 1), 17 male meiotic I (Fig. 2), 4 oogonial (Fig. 3) and 3 female brain cells



Figs. 1-6. Photomicrographs of chromosomes of *Sonthonnaxia maenas*.

Fig. 1.	Spermatogonial metaphase showing 62 chromosomes and a B-chromosome (arrow).
Fig. 2.	Metaphase I (♂) showing 31 bivalents and a B-chromosome (arrow).
Fig. 3.	Oogonial metaphase showing 62 chromosomes.
Fig. 4.	Mitotic metaphase from brain cell (♀).
Fig. 5.	Late pachytene (♀) with 31 achiasmatic bivalents.
Fig. 6.	Sex chromatin (arrow) in interphases (♀ germ cells).

(Fig. 4). All the chromosomes intergrade in length. In the males at metaphase I (Fig. 2) the bivalents appear dumb-bell shaped with terminalized chiasmata while in the female, they are achiasmate, as observed at prophase (Fig. 5).

A spheroid, positively heteropycnotic body (sex chromatin) has been observed in interphase cells of gonads (Fig. 6) and brain in the female; in the polyploid cells, however, 2 to 4 such bodies or a single large fused one, have been observed.

A single supernumerary or B-chromosome has also been found to be present in all the mitotic (Fig. 1), prometaphase and metaphase I (Fig. 2) cells in both the males studied. In the lone female studied, the B-chromosome was not observed in any of the seven cells at mitotic metaphase. The B-chromosome shows the following characteristics: 1) its size is much smaller than the smallest chromosome of the normal complement, 2) it exhibits negative heteropycnosis at metaphase I and 3) it does not associate with any of the chromosomes of the complement.

Discussion

The chromosome number in *Sonthonnaxia maenas* is n = 31 which also corresponds to the modal number, suggested for the genera, *Actias, Antheraea* and *Cricula* of the tribe Saturniini (Narang and Gupta, 1979a). The positively heteropycnotic sex chromatin present in the interphase cells of the female of *S. maenas* is likely to represent the Y chromosome as suggested earlier for some other silkmoths (Gupta and Narang, in press). However, sex chromatin is absent in females of another tailed silkmoth, *Actias selene* (Gupta and Narang *loc. cit.*), the chromosome number of which in females is yet to be discovered.

The single extra chromosome present in *S. maenas*, found in all cells of two out of the three individuals studied, has been interpreted as a B-chromosome on the basis of following evidences: 1) very small size unlike the other chromosomes, 2) non-homology with the other chromosomes as evident by absence of any association with them and 3) its peculiar heterochromatic nature characterized by negative heteropycnosis at metaphase I. The B-chromosome of this species, however, seems to be mitotically stable since its number has been found to be invariably one in all the mitotic and meiotic I cells studied. This is the first clear report of B-chromosome in Saturniidae. However, supernumeraries or B-chromosome have also been reported in some species of the Pieridae (*vide* Bigger, 1978) and one species (*Euphydryas colon*) of Nymphalidae (Pearse and Ehrlich, 1979).

Further studies on population cytogenetics of different Saturniids, making use of the available modern smear techniques, are warranted to unravel the presence of B-chromosomes.

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A New Subspecies of *Hemileuca maia* from Central Texas (Attacidae, Hemileucinae)

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The following paper describes a central Texas population of *Hemileuca maia* (Drury) which, although long represented in collections by a substantial number of specimens, has never been distinguished from the nominate subspecies. The characteristics of these Texas populations have become evident to me by abundant material collected in recent years by Roy O. Kendall and Richard S. Peigler.

Hemileuca maia peigleri new subspecies

Types

Holotype ♂ (Fig. 1): Texas, Bexar County, San Antonio, Ebony Hill Research Station, 24-XI-1978, netted 1240 hrs Central Standard Time, R. S. Peigler.

Allotype ♀ (Fig. 2): Texas, Bexar County, northern San Antonio near Helotes, *ex larva* on *Quercus fusiformis*, 16-XI-1963, R. W. & E. S. Quillen (*ex* collection of R. O. Kendall).

Paratypes: Collection of R. S. Peigler: 3 ♂, Brown Co., Lake Brownwood State Park, *ex larva* on *Q. fusiformis*, 13-20-X-1978, collected under Texas Parks Permit no. 20-78; 5 ♂, 1 ♀, Mills Co., ca. 8 km east of Goldthwaite, *ex larva* on *Q. fusiformis, Q. texana,* and *Q. havardii*, 2-27-XI-1978; 2 ♂, Bexar Co., San Antonio, Ebony Hill Research Station, netted 24-XI-1978. Collection of R. O. and C. A. Kendall: 7 ♂, 5 ♀, Brown Co., Lake Brownwood State Park, *ex larva* on *Q. fusiformis*, 29-X-6-XI-1978; 5 ♂, 4 ♀, Mills Co., *ex larva* on *Q. fusiformis*, 15-24-XI-1975; 8 ♂, 4 ♀, Bexar Co., San Antonio, 422 W. King Highway, *ex larva* on *Q. shumardii*, XI-1964, R. W. & E. S. Quillen; 9 ♂, 3 ♀, Bexar Co., north of San Antonio, Helotes, *ex larva* on *Q. fusiforma*, 12-16-XI-1963, R. W. & E. S. Quillen; 1 ♂, 2 ♀, Bexar Co., north of San Antonio, Bacon Road, *ex larva* on *Q. fusiformis*, 14 and 21-XI-1956; 1 ♀, Bexar Co., north of San Antonio, 19-XI-1961; 2 ♂, Bexar Co., San Antonio, Ebony Hill Res. Sta., 1 and 2-XII-1978. Collection of Texas A&M University: 1 ♂, Lampasas Co., Lampasas, 18-XI-1939; 2 ♂, Menard Co., 20-XI-1972, J. W. Stewart; 1 ♀, Sutton Co., Sonora, 25-IV-[larva?]-1932, S. E. Jones; 1 ♂, Kerr Co., Kerrville, 16-XI-1965, Hoffmann; 14 ♂, Bandera Co., Bandera, 20-22-XI-1938, C. E. Heard; 1 ♂, north Bexar Co., 4-XII-1934. Collection of National Museum of Natural History: 3 ♂, Sutton Co., Sonora, on oak leaves (Bish. #14198); 1 ♀, same locality, emerged 16-XI-1935, coll. Babcock. Collection of American Museum of Natural History: 1 ♂, Gillespie Co., Fredericksburg, coll. F. H. Rindge; 2 ♂, Texas (Purchase C. L. Pollard); 1 ♂, Texas, G. D. Hulst. Collection of Los Angeles County Museum of Natural History: 1 ♂, Kerr Co., Kerrville State Park, 8-XI-1964; 5 ♂, 1 ♀, Bexar Co., San Antonio, 17-XI-1963, R. O. Kendall. The holotype and allotype have been deposited in the American Museum of Natural History. Some of the paratypes of the collections of Kendall and Peigler were also deposited in the Museum national d'Histoire naturelle (Paris).

Imago (Fig. 1 ♂, 2 ♀)

Expanse of male: 45-57 mm (length of forewing: 24-31 mm), expanse of female: 54-67 mm (length of forewing: 27-32 mm).

The subspecies differs from the nominate subspecies (Fig. 3 ♂, 4 ♀) by the semi-transparentness of the four wings, giving a glossy and varnished appearance, especially in male specimens.

The covering of scales, of which the feeble density can clearly be seen by examination with the scanning electron microscope (Figs. 5, 6) is of great fragility. The scale cover tends to disappear in specimens which have flown (Fig. 8). Flown specimens become almost entirely transparent, unlike *H. m. maia* in which the wings of worn individuals conserve, at least in some regions of the wing, a certain opaqueness. Observations under high magnification show that, at the time of shedding, the scales are not pulled out but merely are broken, a little portion remaining above the base. The mechanism is the same in both subspecies but the effects are much more striking in *H. m. peigleri*.

The variation of the ornamentation, and more particularly the size of the white median band of the four wings, is the same as in *H. m. maia*; as in them and *H. lucina* Henry Edwards the white bands of the forewings tend to be wider on the ventral surface than on the dorsal surface.[1]

Early Stages

Larva: Comparison of the larva of the sixth instar[2] of *H. m. maia* and *H. m. peigleri*, according to material originating respectively from

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[1] This character is pointed out by Ferguson (1971: 115, 122).

[2] In principle, the final stage. But since in the early instars the larvae all molt simultaneously, regardless of their size, some of them may be very late in growth when most of the others are full grown, so that they need one or even two supplementary molts to reach pupation; the duration of the larval stage can thus be prolonged by several weeks.

Baton Rouge (campus of Louisiana State University), Louisiana, and Mills Co., Texas (8 km east of Goldthwaite), gave differences as shown in Table 1.

TABLE 1

Differences between mature larvae of the two subspecies of *Hemileuca maia*

Characteristic	*H. maia maia*	*H. maia peigleri*
Subdorsal tubercles of metathoracic segment and abdominal segments 1 to 7; dorsal tubercle on abdominal segment 8	White branches	Yellow branches
Other tubercles	Principal spine red, long	Principal spine blackish, clearly shorter
Mottling on epidermis	Light gray	Ivory
Subspiracular line	Vague	Contrasting
Head capsule, thoracic legs and anal plate	Garnet red	Orangish

Pupa: The rim situated on the anterior edge of each of abdominal segments 5 to 7 is at least twice as wide in *H. m. peigleri* (Fig. 9) than in *H. m. maia* (Fig. 10); the zone of abdominal segment 8 in *H. m. peigleri* has much more accentuated teeth and the ventral face of this segment is more rugose.

Ethology

The behavior in the different phases of the preimaginal and imaginal life appears identical in both subspecies. The following notes were extracted from the personal notes of R. O. Kendall and R. S. Peigler.

Hibernation is in the egg stage. Eggs are deposited on a twig of the host plant such that they form a ring composed of numerous eggs. The main host is *Quercus fusiformis* Small; the larvae are also found on other species of oak such as *Q. shumardii* Buckley, *Q. texana* Buckley, and *Q. havardii* Rydb. In nature the larvae hatch in February/March and continue their development until May/June. They are gregarious until the fourth stage, and are frequently parasitized, notably by:

Diptera: Tachinidae
    Spoggosia floridensis (Townsend) (det. C. W. Sabrosky)
    Belvosia bifasciata (Fabricius) (det. C. W. Sabrosky)
Hymenoptera: Ichneumonidae
    Enicospilus texanus (Ashmead) (det. R. W. Carlson)

Pupation occurs in the soil, among dead foilage or slightly below the surface, the pupa enveloped by a mesh of very loose silk. The diapause is in summer but some persist with a hibernation, emerging in the autumn of the following year.

The adult flies during the entire month of November, especially the second fortnight, and into early December. The emergence takes place generally in the morning; in captivity the insect searches feverishly for a horizontal support on which to expand its wings, requiring a long period (30-45 minutes) for expansion after emergence; I have noticed the same for *H. m. maia*, unusual for Attacidae. Flight is diurnal, especially during sunny times (but Peigler has also observed the time covered), of approximately 930 hrs to 1500 hrs. The moths often fly high and rapidly, so that generally many more are seen than can be netted.

Geographical Distribution

Hemileuca maia peigleri is only known at present from the following counties of central Texas: Brown, Mills, Lampasas, Menard, Sutton, Kimble, Gillespie, Blanco, Kerr, and Bexar (Fig. 11). It is probably endemic to the Edwards Plateau, consisting of calcareous hills with *Q. fusiformis*. A female in the Kendall collection from southern Oklahoma (Logan County) was sent to me with the type material; the


1


2


3


4

Fig. 1. *Hemileuca maia peigleri*, holotype ♂, Texas, Bexar County, San Antonio, Ebony Hill Res. Sta.

Fig. 2. *H. maia peigleri*, allotype ♀, Bexar County, northern San Antonio near Helotes.

Fig. 3. *H. maia maia* ♂, Louisiana, Baton Rouge, campus of Louisiana State University.

Fig. 4. *H. maia maia* ♀, same locality.

determination of this single specimen requires confirmation. A male labeled "Texas" (without further locality data) from the National Museum of Natural History, is a typical *H. m. maia*; the occurrence in eastern Texas of the nominate subspecies, very abundant in Louisiana at certain places (e.g., Baton Rouge), would not be surprising.

Because of the semi-hyaline aspect of the wings, in combination with the wideness of the white bands, *H. m. peigleri* has been misdetermined as *H. nevadensis* Stretch in some collections. The latter species possible extends as far east as western Texas, but certainly not central Texas where *H. m. peigleri* occurs, where Kendall and Peigler have intensively collected.

Discussion

Hemileuca maia, *H. nevadensis*, and *H. lucina* form a very homogeneous group of three phenotypically close species, but having three different host plants, respectively *Quercus*,[3] *Salix*, and *Spiraea*. Although *H. m. peigleri* has a host of oak like *maia* and it is phenotypically closest to this species of the genus, it is natural to ask, because of its geographic isolation in a very particular biotope and with constant differences in the preimaginal stages, if it is a distinct species.

The geographic isolation does not accompany an obligatory modification of the genetic constitution and I cite in a recent work (LeMaire, 1978: 16) the example of a very disjunct range of *Paradaemonia ruschii* May & Oiticica of which the only two known localities are about 5000 km apart. The development or maintenance of isolated populations is always common in Attacidae, which are known to adapt to very diverse environments. Species such as *Arsenura armida* (Cramer), *Eacles imperialis* (Drury), and *Titaea tamerlan* (Maassen), live in tropical rainforests as well as semi-arid zones. Quite often the modification of the ecological conditions is not very conducive to subspeciation and it would therefore be hazardous in the case of *peigler*, considering the extensive range of *maia*, to arrive at the conclusion of the species level.

The differences regarding the external morphology of the larva and pupa should also be interpreted with care. Ferguson (1971: 117) reported notable geographic variation in the larva of *H. maia*; in the figure in Packard (1914: pl. 22) the larva does not exactly resemble those from Baton Rouge which I have compared to *peigleri*. It is possible that the modification of the pupa is attributable to an ecological factor, such as the nature of the soil; the enlargement of the

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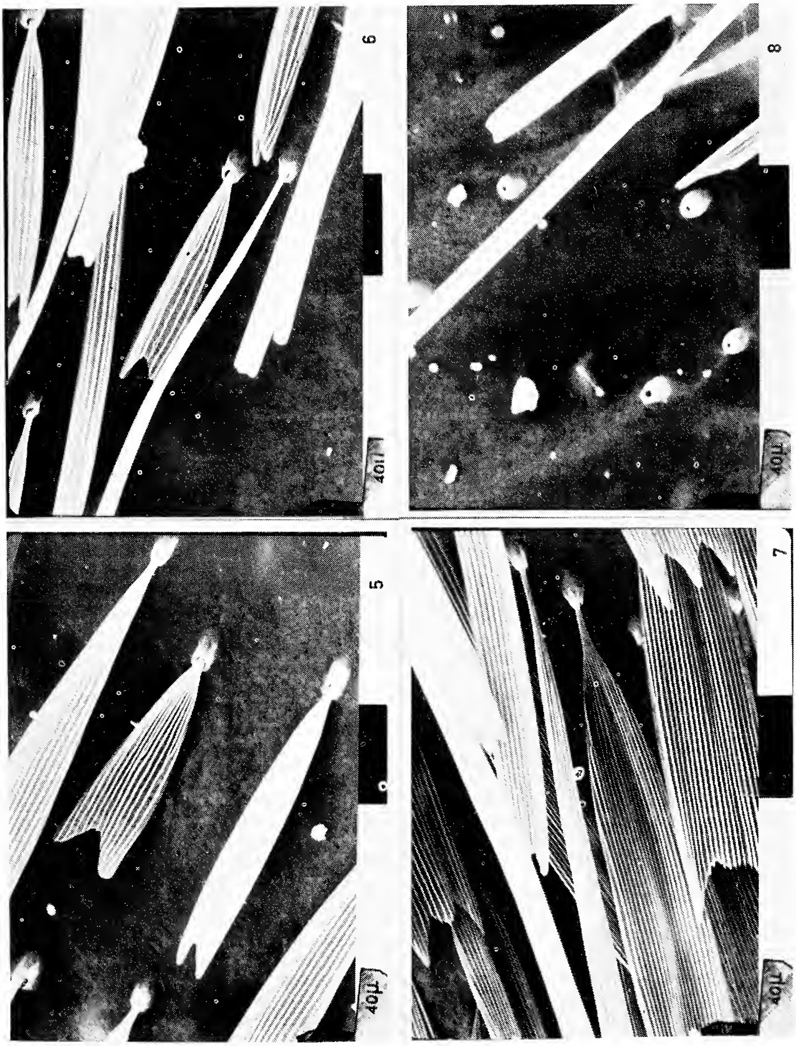
[3] According to Ferguson (1971: 116), it is possible that an Illinois population, reported as *H. maia*, lives on willow.



Figs. 5-8. Wing scales of *Hemileuca maia* viewed with scanning electron microscope (500x).

5-6. *H. maia peigleri* ♂, *ex-larva*, Mills County.

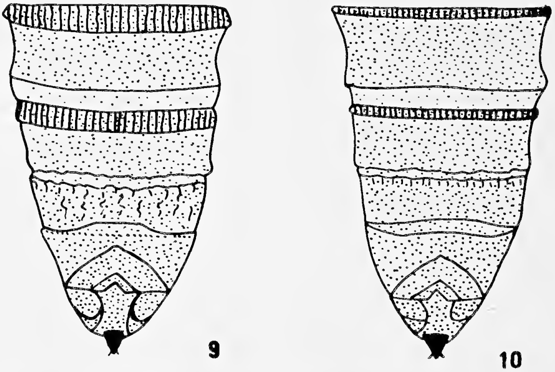
7. *H. maia maia* ♂, *ab ovo*, Baton Rouge.

8. *H. maia peigleri* ♂, Bandera County (wild collected).

rim on the anterior edge of abdominal segments 5 to 7 also occurs in *H. grotei* Grote & Robinson which shares the same biotope.

The similarity in structure of the genital armature cannot be used as an argument in favor of conspecificity of *peigleri* and *maia*, because I fail to find constant differences between the genital armature of these and that of *H. nevadensis* and *H. lucina*,[4] which are certainly distinct species.

The most plausible hypothesis is that *peigleri* is a subspecies of *maia*. I consider as a most important feature that the variation of the ornamentation will be found to be identical in the two taxa, since this type of character seems to be especially significant in the group concerned, i.e., the three species of *Hemileuca*. The status adopted should be rather easily confirmed or reputed by hybridization experiments, considering the ease with which such crosses may be obtained.



Figs. 9-10. Pupae of *Hemileuca maia*, schematic view of the last abdominal segments, ventral view.
9. *H. maia peigleri* ♂.
10. *H. maia maia* ♂.

Acknowledgements: The credit for the discovery of the new subspecies belongs entirely with Richard S. Peigler and Roy O. Kendall who, having a long and constant interest, have collected the majority of the type material forming the basis of the present article. I owe the opportunity of being able to present the description to their kindness and unselfishness in being the authors themselves, together or separately.

I also thank the following: Dr. Douglas C. Ferguson (National Museum of Natural History), Dr. Frederick H. Rindge (American Museum of Natural History), and Mr. Julian P. Donahue (Los Angeles County Museum) for having gladly sent me the Texas specimens from these institutions; the examination of this material was of

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[4] In specimens which I have examined, I have not been able to verify the differences which distinguish the genital armature of *H. lucina* according to Ferguson (1971: 122).

extreme use in comparing with that of Kendall and Peigler. The scanning electron microscope photographs were produced at the Laboratoire d'Entomologie generale et appliquee of the Museum national d'Histoire naturelle (Paris) by Mr. Jacques Boudinot.

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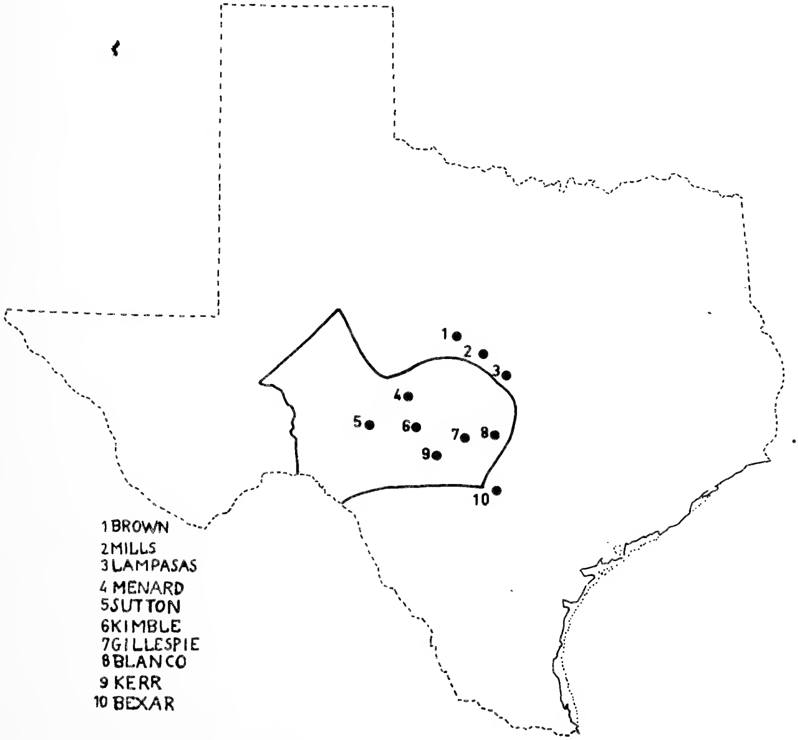

Fig. 11. Map showing known distribution of *H. maia peigleri* with a list of Texan counties for which it is recorded. The unbroken line indicates the boundaries of the Edwards Plateau.

Journal of Research on the Lepidoptera 18(3): 220, 1979(81)

Book Review

Phylogenetic Analysis and Paleontology.
Edited by Joe Cracraft and Niles Eldredge. Columbia University Press, New York, 1979. 233 pp. $ . .

Lepidopterists who are not regular readers of *Systematic Zoology*, that most arcane of journals, may be dimly aware that a new controversy is raging in systematics ver an approach known by its founders as"phylogenetic systematics" and by most people as "cladistics." In many ways, the action is a replay of the bitter strggle over "phenetics" or "numerical taxonomy" in the 1960s. All the ideological passion, the self-righteousness, and the talking past the other side are there, but the cast has been changed. Cladistics is a deductive method for inferring phylogenetic relationships and ordering taxa on this basis. It has made claims of testability in a rigorous, Popperian sense, although its conclusions ultimately depend on minimizing the number of contradictions in accordance with Occam's razor - which is treated as a "given." The method predisposes to splitting and the creation of not only new taxa but new rankings. If all of this strikes you as incomprehensible gobbledygook it would be a good idea to read this book. Although Lepidoptera are never mentioned and the book is ostensibly about paleontology, it contains some of the clearest arguments pro and con the cladistic approach to appear thus far, even though the pro and con speakers seem mostly to have not understood one another at the symposium. Although its rigid formalism is certain to crumble, cladistics will leave its mark on the way most of us do systematics. Its logic will be absorbed just as conventonal systematics co-opted the numerical techniques of the pheneticists while their ideology wasted away. Systematics will probably be better for it, but in the meantime this book can help explain the turmoil. As A. J. Boucot says in the concluding chapter, "all of us ...have seen our favorite stories go up in smoke time after time. We try to console ourselves that each scheme is a better approximation of the ultimate evolutionary 'truth' than the last house of cards..."

Arthur M. Shapiro, Department of Zoology, University of California, Davis, CA 95616.

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Cover Illustration: Wing scales of *Hemileuca maia* viewed with scanning electron microscope (500X). C. LeMaire, pages 212-219.

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Rearing Butterflies on Artificial Diets

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Abstract. Although the literature concerning artificial diets for moths is voluminous, few diets have been reported for butterflies. In this paper I have briefly examined the principles of diet formulation and give details of a diet which has proved successful for a range of species.

Introduction

Butterflies and moths are reared in captivity for a number of diverse reasons and it is therefore not surprising to find a range of techniques recommended in the literature. For the collector who requires only a few mint specimens for the cabinet, it may suffice to confine a wild-caught gravid female with potted foodplant and rear the resulting ova through to imagines thereon. Alternatively, the immature stages may be kept in closed containers and be regularly supplied with fresh foodplant, or simply "sleeved" - enclosed in a tube of netting - over a growing tree or shrub. Unfortunately, these methods are labour-intensive, require much space, and are therefore unsuitable for workers who require large numbers of insects. Further, there may be problems with foodplant availability and it is difficult to effectively control outbreaks of disease. Yet mass-rearing is a prerequisite for the study of most problems of applied entomology.

Bottger (1942) was the first to raise a lepidopteran, *Ostrinia nubilalis* (Huebn.), on artificial diet. The pink bollworm *Pectinophora gossypiella* Saunders, a well-known agricultural pest, was the first phytophagous insect reared on a wheat germ based artificial diet by Vanderzant and Reiser (1956a, 1956b). Since that time numerous diets have been developed for a wide range of moth species, especially those of economic importance; these diets have been collected into useful reference work by Singh (1977). However, few butterfly species have been reared on such diets - Singh (*loc. cit.*) lists only twelve species and these, too, are largely injurious to crops.

This paucity is probably due to a lack of commercial interest in butterflies, but experience has also shown that butterflies are in general somewhat more difficult to rear on artificial diets than are moths. But the difficulties are not insuperable and with a little experimentation most species can probably be reared in this manner. The purpose of this paper is not to present a universal pabulum for larvae, but rather to encourage experimentation.

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One of the first diets to show spectacular results with butterflies was that of David and Gardiner (1965). This was originally developed for the pest species *Pieris brassicae* (L.), but subsequently proved suitable for a range of other species with diverse feeding habits. Like many others, however, this diet is chemically quite well defined and therefore involves careful weighing and mixing of rather a large number of components. Although defined diets are essential for nutrition research, if the aim is simply to rear butterflies it is probably more convenient to use rather crude ingredients and accept that the results may not be reproduceable. This simplifies the diet and reduces costs.

The most successful of over forty diets I have tested since 1974 is detailed in Table 1. It is similar to that of Shaver and Raulston (1971) and has proved suitable for the species listed in Table 2. The diet produces reasonable results for such species, but is probably ideal for none and can undoubtedly be further improved and simplified. In the hope of encouraging this work, I shall try to explain the rationale behind the formulation, although the role of complex materials such as wheat germ and yeast extract is oversimplified in the following account.

Formulation of Diets

Like other animals, butterfly larvae require sources of protein, carbohydrates, lipids, vitamins, minerals and water. For the protein source many authors employ casein or milk powder, but I prefer soy flour since it is cheaper. Carbohydrates are supplied as sucrose or other sugars. Lipids are provided by wheat germ and the dried leaves, but corn oil may also be used at about 0.15% w/w. For some species the dried leaves may be omitted and in such cases corn or raw linseed oil must be added to prevent poor wing development. Vitamins may be added as a stock solution (as in the David-Gardiner diet), but it may be more convenient to use yeast or yeast extract. Minerals are best supplied by commercial salt mixtures such as Wesson salts. In addition, for most species one needs to add ascorbic acid (vitamin C) and choline.

Although the above may be nutritionally satisfactory, we have yet to induce the larvae to feed. Most species require a phagostimulant to bring about this behaviour. This is often some component peculiar to the foodplant, but may simply be sugar. The problem is usually solved by adding dried foodplant material at about 1.5 - 2.0% w/w, but much research is needed in this field. In some reports up to 40% plant material has been incorporated into the diet.

The diet must also possess the correct physical properties. It must contain water, but free water will usually result in the larvae drowning. It must be solid, but not too hard for the rather delicate mouthparts of young larvae. Clearly, some type of gelling agent is required. Gelatin is usually unsatisfactory due to its poor storage properties, and agar is therefore used despite its higher cost. In fairly refined diets one should also add cellulose powder to provide bulk, texture and roughage.

We now have the basis of a diet, but there are a few useful extras. The agar produces a firmer, more brittle gel if potassium hydroxide is added. The pH of the diet is corrected by adding acetic acid. Since food for larvae is also food for microorganisms, potassium sorbate and methyl parahydroxybenzoate are added to reduce spoilage caused by fungal contamination. This reduces the need to sterilize the diet, but a formalin solution may be added providing care is taken to ensure that no trace remains in the diet when it is given to the larvae (it will evaporate from the warm diet). Finally, the risks of infection by the bacteria *Bacillus thurigiensis* may be reduced by adding the antibiotic aureomycin (chlortetracycline).

Preparation

How the diet is prepared may affect both its nutritional and physical properties. As a general rule, use fresh materials, finely ground, and mix thoroughly. The plant material should be carefully selected, washed and then oven-dried at 110 degrees C until it powders readily (10-30 min). The aim is to dry it as quickly as possible so that little volatile material is lost. The material is then ground (a coffee grinder is useful) and passed through a 0.5 mm mesh screen.

The agar is stirred into about 60% of the distilled water and then boiled for 3-10 min, with stirring. Ideally, this should be done in a steam bath to avoid burning the agar, but with care it may be done over direct heat. Allow the solution to cool to 75-85 degrees C.

Meanwhile, thoroughly mix the remaining solids in the rest of the distilled water (use a liquidizer if possible) and then add the cooled agar with further blending. The cooling serves to reduce decomposition of heat-labile substances, although the pH and protective action of other parts of the diet also help in this way. Next, add the liquids in order with 2 min blending between each addition. Finallv, dispense the warm diet to containers, cover with clean paper towels, and leave to dry slightly for 24 h.. The diet may then be stored almost indefinitely at 4 degrees C - bring to room temperature before use. If required, the diet may be autoclaved (a domestic pressure cooker is fine) without deleterious effects.

Containers and Rearing

The provision of suitable clean containers is an important part of rearing. For small larvae, plastic pots with card lids, such as creamers, are ideal and readily available from catering suppliers. Later one may use disposable drinking cups or glass jars (which may be sterilized for re-use). Do not overcrowd the larvae, and avoid excessive condensation by reducing numbers or fitting more permeable lids. Polystyrene cups are ideal for rearing, pupation and adult emergence due to the rough surface providing footholds.

It is advisable to start the rearing programme with ova, since larvae which have fed on normal foodplant may refuse the diet. Where possible, the ova should be removed from the plant using a fine brush, or by washing with water containing a little surfactant (0.2% Teepol) and bleach (1% sodium hypochlorite) at 20-25 degrees C. The latter also serves to surface-sterilize the ova, but may kill some. After 10 min wash twice with equal volumes of water, and collect the ova on filter paper. The ova are then transferred to the diet by means of a fine brush, or they may be stored in plastic containers until they hatch and the young larvae similarly transferred.

For many species the diet may simply be poured into the rearing containers to a depth of at least 0.5 cm, with a thin film on the sides. For others, especially edge-feeders, the diet may be shredded using a cheese grater. A further possibility, if the diet is not sterile, is simply to cut a piece from the block and press it firmly into the pot using clean paper towels. This provides a rough surface suitable for most feeding habits and also helps dry the surface slightly.

Newly-hatched larvae may wander for up to 24 h, and the acceptance varies from about 30-100% depending on species. Generally, members of the family Lycaenidae are the most difficult. In most cases progeny from insects reared on the diet settle more readily than their parents; one is evidently applying selection pressure.

The containers can be inverted to prevent frass fouling the surface of the diet although this may not be necessary. The temperature and light regime will obviously vary with the species and the aims of the investigator. A steady 20-25 degrees C in darkness is suitable for many species. The larvae should be transferred to fresh diet weekly, and one should aim to keep the density of larvae in each pot such that nearly all the diet is consumed in this period. For pupation, the pots may be turned lid uppermost so that the prepupae are formed there, or the container may be lined with paper or card (if polystyrene cups are not used).

Cannibalistic species present special problems, but many are well-suited to artificial diets since they settle readily; presumably a reflection of their catholic tastes regarding food sources. One may use a container for each individual larva, but this is costly and time-consuming. Shredded diet may be used to provide refuges in the food itself, so that a number of larvae may be kept in each container. This wastes diet, but it may be cheaper than providing more pots and filling each one with diet. Some larvae will be lost, and the optimum density of larvae per pot will have to be determined by experiments. Often high temperatures and humidity lead to increased cannibalism, so these variables should be kept in mind. This method is used for commercial production of both *P. gossypiella* (Mattoni, personal communication) and *Heliothis virescens* Fab. (Morton, unpublished) in the U.S.A.

An alternative is to pour the diet into trays and then press in a grid to provide a number of individual cells, much like an egg-box. Light diffusion grids and aluminium honeycombs are ideal for these purposes, and may be sterilized for re-use in strong bleach solution. This method has been used for *Heliothis* spp. (Raulston and Lingren, 1969; Raulston and Shaver, 1970), *P. gossypiella* (Morton, unpublished), and several butterflies.

Subsequent pairing and oviposition are unaffected by the use of artificial diet techniques, and these steps in the cycle may therefore prove to be the most difficult aspects of the whole rearing procedure. However, it is now possible to try to rear all year round, since the seasonal availability of larval foodplant is no longer a serious problem (although for most species some plants will still be needed to provide ovipositing stimuli). Similarly, one may tackle species which use plants that are not indigenous or readily available. Very large broods may be reared under almost identical conditions, facilitating investigation of problems in genetics and physiology. Finally, specimens may be easily obtained from a single wild female, thus reducing the possibility of damage to populations or habitat by excessive collecting. With regard to conservation of gene pools, it is now feasible to maintain laboratory populations considerably larger than those occurring in the wild (Morton, in print).

Those who feel unable or unwilling to prepare these diets themselves may be interested to know that plans are being laid by a private concern to market these products in aid of the Lepidoptera Research Foundation; the proceeds will be used to support field and laboratory research.

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Table 1

Composition of artificial diet for butterflies (listed in Table 2).

Solids	**% Composition (w/w)**
soy flour	7
wheat germ	6
yeast extract	6
sucrose	3.6
dried plant material	1.5
Wesson salts	1
ascorbic acid	0.4
potassium sorbate	0.2
methyl parahydroxybenzoate	0.15
aureomycin (veterinary grade)	0.023
agar	1.9
Liquids	
formaldehyde solution (10%)	0.43
potassium hydroxide (4M)	0.8
acetic acid (25%)	1.14
choline chloride solution (50%)	0.23
distilled water	to mass

Table 2

Species successfully reared on the artificial diet detailed in Table 1.

Hesperiidae

- *Pyrgus malvae* L.
- *Erynnis tages* L.
- *Thymelicus lineola* Ochs.
- *T. sylvestris* Poda (= *flavus* Breunnich)
- *Hesperia comma* L.
- *Ochlodes venata* Brem. & Grey

Papilionidae

- *Papilio machaon* L.

Pieridae

- *Leptidea sinapis* L.
- *Pieris brassicae* L.
- *Artogeia rapae* L.
- *A. napi* L.
- *Anthocharis cardamines* L.
- *Colias crocea* Geoffroy
- *C. eurytheme* Bsdv.
- *Gonepteryx rhamni* L.

Lycaenidae

- *Thecla betulae* L.
- *Quercusia quercus* L.
- *Strymonidia w-album* Knoch
- *Callophrys rubi* L.
- *Lycaena phlaeas* L.
- *Cupido minimus* Fuessly
- *Celastrina argiolus* L.
- *Plebejus argus* L.
- *Aricia agestis* Denis & Schiff.
- *Lysandra coridon* Poda
- *L. bellargus* Rott.
- *Polyommatus icarus* Rott.

Riodinidae

- *Hamearis lucina* L.

Heliconiidae

- *Agraulis vanillae* L.

Nymphalidae

- *Limenitis camilla* L.
- *Inachis io* L.
- *Cynthia cardui* L.
- *Vanessa atlanta* L.
- *Aglais urticae* L.
- *Polygonia c-album* L.
- *Argynnis paphia* L.
- *Mesoacidalia aglaja* L.
- *Fabriciana adippe* Schiff.
- *Clossiana euphrosyne* L.
- *C. selene* Denis & Schiff.
- *Eurodryas (Euphydryas) aurinia* Rott.

Satyridae

- *Melanargia galathea* L.
- *Hipparchia semele* L.
- *Maniola jurtina* L.
- *Aphantopus hyperantus* L.
- *Pyronia tithonus* L.
- *Coenonympha tullia* Meuller
- *C. pamphilus* L.
- *Pararge aegeria* L.
- *Lasiommata megera* L.

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Taxonomic and Biological Notes on *Bellura gortynoides* Walker (Noctuidae)[1]

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Abstract. A taxonomic review is given for *Bellura gortynoides* Walker and related species. The biology of *B. gortynoides* is reviewed with new observations. The mature larva and pupa are described and illustrated.

Introduction

Bellura gortynoides Walker is one of the few Lepidoptera species that pass through their immature stages in an aquatic or semiaquatic environment. The taxonomic history of *B. gortynoides* and its related taxa is complex and confusing. The thirteen species described in this group of noctuids have been variously referred to as *Edema, Sphida, Arzama,* and *Bellura.* The taxa were primarily separated by the male frons, the color of the adult female anal tufts, and the presence of tubercles on the larval vertex (Hampson, 1910; Forbes, 1954). The usefulness and validity of these characters has since been refuted (Barnes and Benjamin, 1923; Forbes, 1954; Levine and Chandler, 1976). According to Levine and Chandler (1976), there are only three valid species, *gortynoides* Walker, *obliqua* (Walker), and *densa* (Walker), in a single genus, *Bellura.* However, the taxonomic problems are still not totally resolved.

Numerous articles deal with the biology of *B. gortynoides* (Center, 1976), but due to past taxonomic confusion, there is considerable doubt as to which apply to this species. Most are old and without precise observations, and in no case has the external morphology of the larva and pupa been studied in detail. Considering the taxonomic state of the group, more thorough studies could prove to be of value in clarification. This paper presents in detail the external morphology of the mature larva and pupa of *B. gortynoides.*

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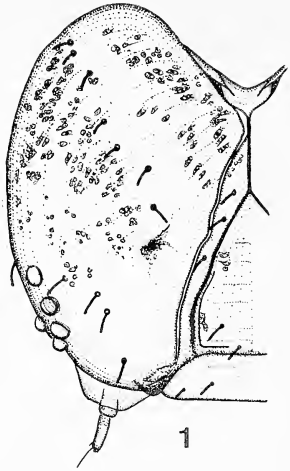
Materials and Methods

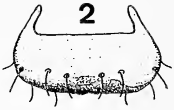
Sixty-two larvae and 34 pupae were examined. These were collected from the following localities in Florida: Alachua Co.: Perry Pond, Biven's Arm, Sante Fe River north of High Springs, pond 1.4 miles east of River Styx off Highway 346; and Putnam Co.: Rodman's Reservoir, pond in Interlachen.

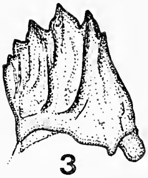
A WILD M-5 microscope and drawing tube attachment was used in making the illustrations. Measurements are based on the average of the available specimens.

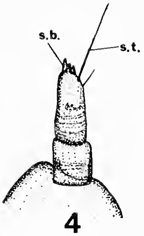
Description of Stages

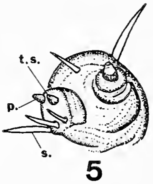
MATURE LARVA: Length: 52 mm, width: 4.8 mm. Head light yellowish brown with irregular, compounded blotches of darker brown varying in shade (Fig. 1); texture noticeably wrinkled, minutely granular; ocelli pigmented dark brown (Fig. 1, 10); mandibles heavily sclerotized with seven teeth, four strong and three weak (Fig. 3); labrum with ventral edge heavily sclerotized, irregularly shaped (Fig. 2); antennae three-segmented, third segment about size of sensilla basiconica, more distal sensillum trichodea four times size of other (Fig. 4); postmentum with ventral pair of short, stout setae (often asymmetrical) and basal sclerotizations; hypopharynx with two pairs of small ventral setae (often asymmetrical), some sclerotization, and dorso-lateral papillae; prementum with partially sclerotized ring, two-segmented labial palp with single preapical sensillum, second segment minute, sensillum-like; spinneret narrow, tapering (Figs. 7, 8); maxillary lobe with four prominent setae, basal largest, terminal lobe with large swelling bearing one pair of papillae and three setae, tip of lobe without tubercles (Figs. 5, 6); height of head: 3.0 mm, width: 3.2 mm. Dorsal view: body pale gray with green hue, somewhat transparent; mid-dorsal stripe gray, weak, darker than background; setae short, brown; extra subanal seta present (Fig. 13); prothoracic shield sclerotized, variable in shape, same color as head, with dark edges, anterior darkest with lateral extensions (Fig. 13); posterior margins of segments appear darker due to folding of integument; integument minutely coarse, much more wrinkled than head; spiracles on eighth abdominal segment larger and dorsad of preceding spiracles, directed caudally due to reduced size of ninth segment (Fig. 13); D2 seta of anal plate 1.3 mm in length (Fig. 12). Lateral view: body above spiracles colored as dorsum, white below; subspiracular stripe colored as mid-dorsal; irregularly arranged patches of light brown spots on dorsal and lateral surfaces of integument approximate setal bases in size, shown on second abdominal segment in Fig. 13; setal patterns on abdominal segments 3-6 nearly identical. third illustrated (Fig. 13); spiracles dark brown, light brown centered, eighth abdominal spiracle largest, followed by prothoracic spiracle, then seventh abdominal spiracle, spiracles 1-6 of equal size (Fig. 13). Ventral view: body white; thoracic legs











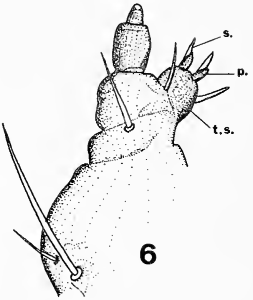


Fig. 1. Frontal aspect of head, 25X

Fig. 2. Frontal aspect of labrum, 25X

Fig. 3. Inner aspect of right mandible, 25X

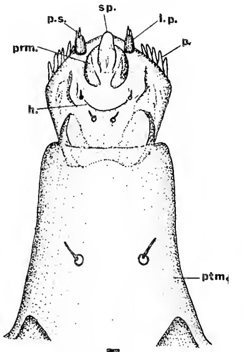
Fig. 4. Ventral view of antenna, 75X; s.b., sensillum basiconica; s.t., sensillum trichodea

Fig. 5. Apical view of maxillary lobe, 75X, s., seta; p., papilla; t.s., terminal lobe swelling

Fig. 6. Ventral view of maxillary lobe, 75X; s., seta; p., papilla; t.s., terminal lobe swelling

light brown with brown claws (Fig. 9); anal prolegs reduced, posteriorly directed (Fig. 13); crochets uniordinal, numbers varying from 17-22 on segments 3-6, 11-14 on segment 10 (Fig.11).

PUPA: Length: 26.5 mm, width: 4.4 mm. Surface glossy; top of head and cremaster black, remainder deep reddish brown; cuticle finely wrinkled, minutely granular, granulation pronounced on posterior halves of abdominal segments 4-7, dorsum with sparse pitting causing integument to appear darkly spotted, top of head and cremaster rough with small, irregular, raised areas; male with encircling, serrated ridges on abdominal segments 5-7, teeth-like processes extending around to dorso-lateral surface; segment 8 with small ridge ventrad, processes posteriorly directed on all segments, processes largest on segment 7 (Figs. 14, 16); female as described for male but ridge on segment 7 not on dorsum and ridge on segment 8 absent; cremaster with 4 hooks, each about 0.5 mm in length (Fig. 15); mesothoracic spiracle three times size of remaining spiracles; eighth abdominal spiracle dorsally located, slightly larger than other abdominal spiracles.



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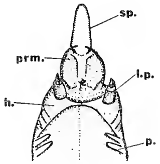

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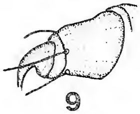

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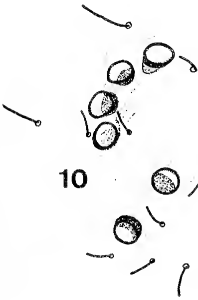

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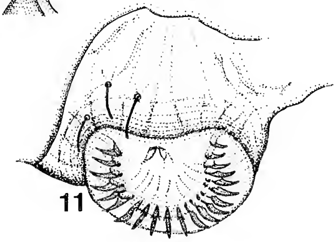

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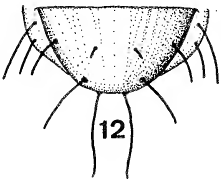

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Fig. 7. Ventral view of mentum, hypopharynx, labial palpi, and spinneret, 75X; hypop., hypopharynx; l.p., labial palp; p., papilla; prm., prementum; ptm., postmentum; p.s., preapical sensillum; sp., spinneret

Fig. 8. Dorsal view of hypopharynx, prementum, labial palpi, and spinneret, 75X; hypop., hypopharynx; l.p., labial palp; p., papilla; prm., prementum; sp., spinneret

Fig. 9. Thoracic claw, 50X

Fig. 10. Ocellar arrangement and setal pattern, 50X

Fig. 11. Crochets, 50X

Fig. 12. Anal plate, 20X

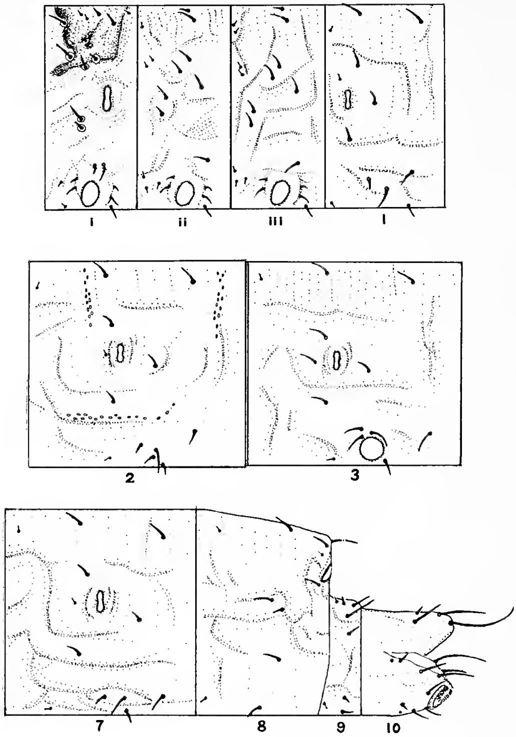

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Fig. 13. Setal maps, 15X

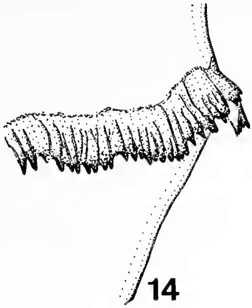
Field Observations

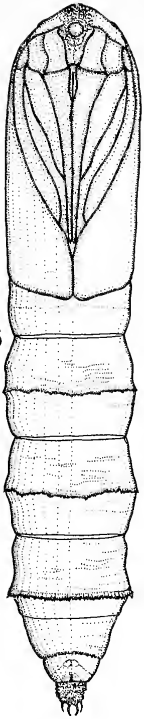
All specimens were collected from *Nuphar luteum* Engelm. or *N. advena* Ait. (Nymphaceae). It appears *N. luteum* has not previously been recorded as a foodplant.

The number of infested petioles consistently increase with water depth in all the localities. Since most plants had only one or two infested petioles, there is probably either wide dispersal of young larvae or a high mortality rate, as each egg mass contains 14-20 eggs.

The pupae were found tightly lodged in their tunnels. This is made possible by the toothed ridges which prevent the pupa from falling down the tunnel. The teeth-like processes are directed posteriorly to allow movement up with the rising water. The tooth ridges may also function to anchor the pupa during adult emergence.

The larva's palatability to fish was investigated by Mr. George Hutchinson, graduate student of the University of Florida, Entomology Depart-





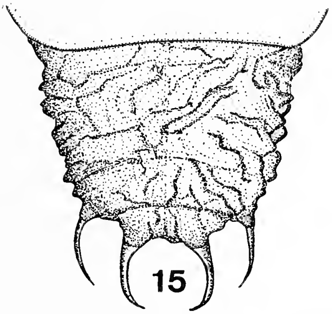


Fig. 14. Enlarged view of seventh abdominal ridge of pupa showing formation of teeth, 50X

Fig. 15. Ventral view of cremaster, 50X

Fig. 16. Ventral view of pupa, 12X

ment, during the fall of 1977. His observations suggest that they are eaten by fish, but only after the fish thoroughly washes the larva.

Other observations included finding adults resting beneath lily pads on surfaces free of water, and leeches occasionally occupying empty tunnels.

Discussion

The ova of *B. gortynoides* are characteristically laid in a mass of one to three layers and covered by the hair from the female's anal tuft. In Indiana, the first generation egg mass averages 14 and the second 20 (Levine and Chandler, 1976). The egg is pale yellow, hemispherical, slightly flattened at one end, with the chorion very finely pitted, 0.50 mm in height and 0.75 in width. The newly emerged larvae feed gregariously as miners on the parenchyma of the leaf. By the end of the second instar, the larva becomes solitary. Before the fourth instar, the larva stops mining and bores either into the midrib or petiole of the leaf, or swims to another leaf, as there is never more than one larva to a tunnel. Their oily epidermis helps to keep them at the water's surface when they are swimming. The larva uses its specially adapted eighth abdominal spiracles when it needs oxygen by merely backing up the tunnel. Feeding is done nocturnally on the upper epidermis and leaf margins. As much as two-thirds of a leaf may be consumed. The number of larval instars varies from six to nine. Pupation occurs near water level and adults emerge in about two weeks. The only authenticated foodplants for *B. gortynoides* are *Nuphar* spp., though, because of its confusing synonymy, species of *Nymphaea, Eichornia, Pontederia* and *Typha* have been reported as hosts. Parasites and predators of *B. gortynoides* have been listed by Levine and Chandler (1976).

Nuphar advena Ait. can be a pest weed that interferes with navigation and causes silting. Levine and Chandler (1976) studied the potential of *B. gortynoides* as a biological control agent for this lily and concluded that it was an unlikely means of control, since the larva does not kill or greatly weaken the plant.

The literature cited includes a complete bibliography of biological informaton that has been published on *B. gortynoides*. It is hoped that the descriptions of the larva and pupa of *B. gortynoides* might stimulate others to use these additional characters to help clarify the taxonomy of *Bellura* species.

Acknowledgments: Our thanks is extended to Dr. George L. Godfrey, Illinois State Natural History Survey--Urbana, for his comments on the chaetotaxy of *B. gortynoides*.

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A New Species of *Automeris cecrops* (Attacidae: Hemileucinae)

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This article deals with the description of a subspecies of *Automeris cecrops* (Boisduval) discovered recently in northeastern Mexico. The type material consists of, in addition to the holotype, a female allotype collected by Richard S. Peigler and the offspring of this female reared in France by the author. The two previously known subspecies, the nominate subspecies and *A. cecrops pamina* (Neumoegen), are localized, the first in the vicinity of Mexico City, and the second in Arizona, New Mexico, and Chihuahua; both live at a higher altitude than the new subspecies.

Automeris cecrops peigleri LeMaire **new subspecies**

Types:

Holotype: ♂ (Fig. 1), Mexico, Nuevo Leon, Laguna de Sanchez, 27-VII-1976 (collection of C. Lemaire < Museum national d'Histoire naturelle, Paris); allotype: ♀, Nuevo Leon, 27 km west of Linares, 500 m, 23-VII-1976, at light, R. S. Peigler; paratypes: 8 ♂♂, 3 ♀♀, *ob ovo* (laid by allotype), reared in France at Gordes (Vaucluse) by C. Lemaire on *Populus alba* L. (10-VIII/XI-1976), emerged 17-VII-12-IX-1977 (all in same collection as holotype, except one pair of paratypes in collection of R. S. Peigler, South Carolina).

Description

♂ (Fig. 1). Expanse: 71-80 mm; length of forewing: 35-41 mm. Antennae rust-colored, frons and top of thorax brown, with a tuft of bright scales at the base of the forewings; abdomen carmine on the dorsal surface, beige on the ventral surface and at the anal extremity. Legs brown passing to rosy gray on the tarsi.

Forewings rather elongate, not falcate, outer edge weakly oblique. Ground color reddish brown, stripes dark brown, the antemedian with a grayish border, forming a very pronounced open angle on the cubitus, the postmedian preceded by a light gray border, scattered with yellow scales, slightly preapical (ca. 2mm) and a little outwardly concave. Submarginal band vague. Discocellular spot slightly darker than the ground color, emphasized with black at the center and on the border.

Median-basal area of the hindwings dark yellow, passing to brown rose below the costa and also to rose toward the anal border. Postmedian line black, very slightly undulating, separated by a beige rose space from the brownish violet submarginal band. Marginal zone of the same tint as the forewing. Ocellus (diameter 9-11 mm), formed partly by a sharp white discocellular streak, by a bluish pupil, scattered with white scales, within a brown black iris, continuous with a black ring.

Ventral side beige, with a rosy zone on the internal edge of the forewings; postmedian line brown rose, weakly contrasting; submarginal bands very vague or imperceptible. Discal spot of forewings formed by a white dot, in the center of a large black ring; small discocellular dot of the hindwings white, finely edged by brown rose.

♀ (Fig. 2). Expanse: 85-93 mm; length of forewing: 43-47 mm. Fundamental brown coloration of forewings darker than in the males but with rose or violet paler zones on the hind part of the median area and on all or part of the external area. Dorsal side of abdomen carmine, with the very contrasting beige rose intersegmental rings. Diameter of the ocellus: 10-12 mm.

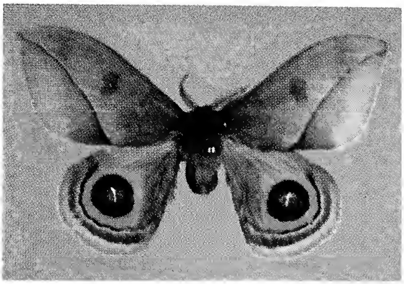
Automeris cecrops peigleri differs principally from the nominate subspecies and from *A. c. pamina* by the much greater diameter (♂ 9-11 mm as opposed to 6-8 mm; ♀ 10-12 mm as opposed to 7-9 mm) of the ocellus which also appears much closer to the postmedian line. The dominant coloration of the upper surface of the wings is much more contrasting than in *A. c. cecrops* in which it varies from light gray to brownish gray and to brown rose or orange, and much darker than in *A. c. pamina* where it passes from light gray to rose gray; yellow area, around the ocellus, darker and zones rose or brown rose, on the subcostal and anal areas of the hindwings, more clearly marked.

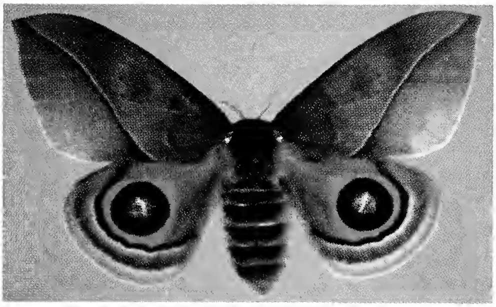
The available material examined is quite homogeneous and the reared specimens do not differ in size or coloration from those which were collected in the wild.

Early stages

Egg white, micropyle emphasized by a very fine black point.

Larva (Fig. 3), in the seventh (last) stage, yellowish green, with, on abdominal segments 1 to 8, a turquoise blue dorsal band, edged by black and, after these and on each side, three subdorsal bands, yellow,





Figs. 1 & 2. *A. cecrops peigleri* n. subsp., holotype ♂. 2, *id.* paratype ♀.
Fig. 3. *A. cecrops peigleri* n. subsp., larva, seventh instar, on *Populus* sp.

turquoise blue edged with black, and yellow, respectively, then a white spiracular line, edged by black, and a subspiracular white line. These different lines and bands are interrupted in the middle of each segment by a yellow ring on which are implanted the tubercles. Ventral surface black, with deep red rings and fine dots of light gray. Head capsule green, spiracles orange, thoracic legs reddish brown.

Tubercles spiniferous, composed of numerous green or black branches,these mainly occurring on the dominant tubercles of the thoracic segments and abdominal segments 8 and 9. The scheme of implantation of the tubercles is the same as that which I figured (Lemaire, 1971: 31, fig. 1) in an earlier work but the subspiracular inferiors of the eighth abdominal segment are reduced to a ciliated punctation and the paranal scoli are present.

Cocoon brown, not very thick, papery, fixed to a twig and enveloped in leaves of the host plant.

The behavior of the larvae is normal for Hemileucinae, strictly gregarious through the first four stages, later dispersing to form groups of smaller and smaller numbers and finally living isolated or nearly so. The varieties of poplars, besides *Populus alba* (of which the young pubescent shoots are not acceptable) were either refused, or accepted with reluctance. Duration of the larval stages: 5 and 6 days respectively for the first two, 9 to 10 days for each of the following, in individuals in which growth was most rapid (55 days total). The emergences of the imagines, after a diapause of over nine months, covered a span of eight weeks, suggesting this taxon is univoltin.

Geographical distribution

The discovery of the new subspecies considerably extends the known range of *A. cecrops.* The nominate subspecies lives in central Mexico and more especially in the vicinity of Mexico City, at altitudes of around 1800 to 2200 m; I have not seen any specimens from further south Mexico nor from Central America where this species was cited as occurring (probably incorrectly) by Ferguson (1972: 168). *Automeris cecrops pamina* has been collected at numerous places in Arizona, at altitudes of between 1300 and 2200 m, and in a locality at 2300 m in New Mexico. It has recently been discovered in Chihuahua, Mexico (Creel, ca. 2134 m) where the larva has been found on *Quercus grisea* Liebm by R. O. and C. A. Kendall in September 1978. *Automeris cecrops peigleri* represents the species in the eastern part of northern Mexico and occurs at low altitudes.

Acknowledgment: It is with particular pleasure that I dedicate this new subspecies to my correspondent and friend, Richard S. Peigler, who is responsible for most of the type material.

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Gynaephora rossii (Curtis) on Mt. Katahdin, Maine, and Mt. Daisetsu, Japan, and Comparisons to Records for Populations from the Arctic (Lymantriidae)

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Abstract. Populations of *Gynaephora rossii* (Curtis), an Arctic and alpine species of Lymantriidae, were studied on Mt. Katahdin, Maine (45.5°N, 68.5°W; 1606 m) and on Mt. Daisetsu, Hokkaido, Japan (43.7°N, 143°E; max. 2289 m) during 15 single-day ascents. Larvae fed principally on ericaceous plants (*Rhododendron aureum* Georgi on Daisetsu, and *Vaccinium uliginosum* var. *alpinum* Bigelow on Katahdin) though roseaceous plants are reportedly eaten in the Arctic. In the laboratory, larvae from both locations fed on *Salix babylonica* L., and Maine larvae also fed on *Potentilla fruticosa* L. Development at the two locations appeared to require 2 or 3 years, whereas in the Arctic, it may take 10 years. Eggs, 1st-, intermediate-, and late-stage larvae, but not pupae, appear able to overwinter. At Daisetsu, egg masses (ave. 79 eggs, max. 139 eggs, n = 7) were positioned on upright woody stems, not on cocoons as reported for the Arctic. Coloration of the mature larvae of the alpine populations differed slightly.

Natural enemies include a parasitic tachinid, *Spoggosia gelida* (Coquillett), a first record outside of the Arctic, and an ichneumonid, *Nepiera* sp., both parasitic on larvae at Katahdin. An unknown ichneumonid pupal parasite (ca. 12% parasitism), a virus disease, and a predatory shrew, *Sorex* sp. occurred at Daisetsu. Populations of *G. rossii* fluctuated unpredictably from one season to the next. Defoliation of *R. aureum* was observed (Sept. 1975) at Daisetsu, and on subsequent ascents, the result was some host plant setback and mortality, therefore changes in floral composition.

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Introduction

Gynaephora rossii (Curtis) is an unusual Arctic and alpine lymantriid, previously known as *Byrdia rossii* (Curtis (Ferguson 1978). This species and a congener are the largest invertebrates living in the northernmost limits of vegetation in the high Arctic (Ryan and Hergert 1977) where they are subjected to environmental extremes. It also occurs on high mountain tops in lower latitudes. Because of the conditions in the Arctic and the probable ability of the insect to overwinter in any larval stage, the life span of *G. rossii* there may require many years. Thus this species, and a congener, "... are probably the longest-lived species of Lepidoptera known" (Ferguson 1978). Inasmuch as *G. rossii* lives in generally inaccessible Arctic or alpine habitats, relatively little biological information is available concerning this species. However, Downes (1962, 64, 65) cited *G. rossii* as particularly well adapted to climatic extremes of Arctic life.

In the Arctic, *G. rossii* occurs from Labrador, across Canada and Alaska in North America, and across eastern Siberia to the Ural Mountains in Asia (Ferguson 1978). In alpine habitats in eastern North America, it occurs on mountains in Quebec, on Mt. Katahdin, Maine (Brower 1974), on Mt. Washington (Dyar 1896) and Mt. Jefferson (Grote 1897) in New Hampshire. In the west, it is recorded from the high Rocky Mountains in Wyoming and Colorado (Ferguson 1978) and in Alberta by Ryan (1977) who illustrated the North American distribution. In Japan, only the Daisetsu Mountains (with several peaks over 2000 m) of central Hokkaido support this moth (Uchida 1936; Inoue 1956, 71); and further west, in the Sajan Mountains, southwestern Irkutsk, USSR, and mountains in Mongolia (Inoue 1965), populations are found of what appears to be the same insect. These Asian forms were described as a separate species, *G. lugens* Kozhanchikov, but this name has now been synomized with *G. rossii* by Ferguson (1978).

We studied *G. rossii* during periodic ascents into alpine habitats of Mt. Katahdin, Maine USA (45.5°N, 68.5°W) and Mt. Daisetsu, Hokkaido, Japan (43.7°N, 143°E) and report here our observations. We also recorded parasites and other natural enemies, compared the 2 alpine populations, and considered the alpine populations in relation to available literature on the Arctic populations.

Methods

Nearly all our information was obtained from direct field observations made during single-day ascents of the mountains. Between 1974 and 1978, Mt. Katahdin, elev. 5268 ft. (1616 m), was climbed 11 times (PWS 4 times, PJC 6 times, jointly 1) and Mt. Daisetsu, Max. 7513 ft. (2289 m), 4 times (PWS). Moreover, *G. rossii* larvae were so abundant during September (Katahdin 1974 and Daisetsu 1975) that a few larvae were returned to the laboratory and reared to obtain information on behavior, feeding preferences, and parasitoids. Also at these times of abundance, the frequency of larval feeding on various plant species was recorded. Notes on abundance, behavior, and life stage were recorded whenever *G. rossii* was encountered. Photographs were taken of feeding larvae, eggs, plant host species, and the general habitats utilized.

Results and Discussion

Host Plants:

Various plant species have been reported fed on by *G. rossii* Tietz (1972) compiled a list for New England populations that included *Betula* sp., *Populus balsamifera* L., *Populus deltoides* Bartr. ex Marsh, *Salix* sp., and *Viburnum* sp. Those listed by Inoue (1971) included *Salix, Rhododendron, Vaccinium,* and *Empetrum.* In the Arctic, *G. rossii* was reported as feeding on *Dryas integrifolia* Vahl, *Saxifraga oppositifolia* L., *Salix arctica* Pallas (Ryan 1974), and *Saxifraga tricuspidata* Rottb. (Scudder et al. 1879).

When we observed the 2 alpine populations feeding and scored those plants being consumed by individual larvae, it appeared that a species of *Vaccinium* and a species of *Rhododendron* were most frequently eaten in mid-September in Maine and Hokkaido. respectively (Table 1). Indeed, ericaceous plants appeared to be a preferred food of both populations and at Daisetsu, when *G. rossii* populations were dense, the *R. aureum* at one site was almost completely defoliated. These feeding preferences are unlike those listed by Tietz (1972) for New England populations or for populations in the high Arctic (Ferguson 1978). Perhaps this is the result of

Table 1

Host plants fed on by *Gynaephora rossii* (Curtis) in two relict populations outside of the Arctic

Mt. Daisetsu, Hokkaido, Japan* (17 IX 75)	
No. Larvae Feeding	
22	*Rhododendron aureum* Georgi (Ericaceae)
6	*Phyllococe caerulea* Babington (Ericaceae)
6	*Geum pentapetalum* (L.) Makino (Rosaceae)
4	*Vaccinium vitis-idaea* Linnaeus (Ericaceae)
2	*Carex* sp. (Cyperaceae)
1	*Salix yasoalpina* Koidz. var. *neo-reticulata* (Nakai) Kimura (Salicaceae)
Mt. Katahdin, Maine, USA* (14 IX 74)	
31	*Vaccinium uliginosum* var. *alpinum* Bigelow (Ericaceae)
3	*Potentilla tridentata* Aiton (Rosaceae)
1	*Vaccinium vitis-idaea* var. *minus* Loddiges (Ericaceae)
1	*Empetrum nigrum* Linnaeus (Empetraceae)

*Plant determinations by Dr. Charles Richards, University of Maine, Orono, Maine and Dr. Koji Ito, Hokkaido University, Sapporo, Japan, for their respective areas.

adaptive shifts in host utilization in these confined relict populations. Generally, a shift toward increasing use of plants in Ericaceae probably would be the result of reduced plant diversity in the mountainous habitats where ericaceous plants are well represented (Tatewaki and Samejima 1959; Lamson-Scribner 1892). In the Arctic, Rosaceae and Salicaceae seem to be utilized most frequently. Brower (1974) collected larvae on *Potentilla tridentata* Ait. (as *P. trifoliata*) on Katahdin.

In a search for additional food plant information, we offered the laboratory held *G. rossii* a variety of related plants. Only *Salix babylonica* L. and *Potentilla fruticosa* L. were acceptable to these larvae. Also three varieties of *P. fruticosa* were tested, and Coronation triumph, Mt. Everest, and Jackmani showed decreasing acceptability, respectively. Ryan (1977) reared larvae in the laboratory on leaves of *Prunus*.

Ferguson (1978) suggested that *G. rossii* was a general feeder. We found larvae were limited to a rather narrow range of host plants by the restricted conditions of alpine environments. Our field evidence suggested that ericaceous plants were preferred (Table 1) despite the presence of other potential food plants (Tatewaki and Samejima 1959; Lamson-Scribner 1892).

Development:

Although the development of *G. rossii* larvae has not been studied in detail in any alpine habitat, Ohyama and Asahina (1971) suggested that it required 2 years on Mt. Daisetsu on the basis of evidence available from collected larvae. We also believe that 2 or 3 years are generally required. Oliver et. al (1964) hypothesized that any instar could overwinter at the onset of unfavorable conditions and that diapause was obligatory in the last instar. Our field evidence supported this first view since, on Daisetsu, we found mature larvae most frequently in September when fewer intermediate-stage larvae were present. Results of our laboratory rearing were contradictory to the second point on obligatory diapause. We found eggs in September which hatched when warmed up only slightly. Thus, there may be an autumn hatch of eggs, and both eggs and 1st-instar larvae may be present in mid-September directly before overwintering. These findings suggest that eggs and/or newly hatched, intermediate, and mature larvae observed in September were overwintering stages in at least one (Daisetsu) of the 2 alpine populations.

In the Arctic, the generation time is considerably longer. On the basis of weight calculations, Ryan and Hergert (1977) concluded that one generation required 10 years. From this information, Ferguson (1978) stated that *G. rossii* has the longest known development period for a moth. There is presently no precise data available concerning the number of instars; however, Ryan (1977) suggested 7 larval molts for *G. rossii* in Arctic populations. In any case the pupae are incapable of surviving temperatures of -20°C (Ohyama and Asahina 1971). Then since ground surface temperatures were frequently lower than that on Daisetsu [min. temperature 5 cm below ground surface: -24°C (Sakai and Otsuka 1970], pupal survival during winter appears unlikely. This further strengthens the theory that overwintering in the last larval stage is obligatory.

The adults are known to emerge shortly after pupating: in early July in both Hokkaido (Inoue 1956) and Maine (Brower 1974). On Devon Island, Canada, adult emergence peaks during July but extends from June through August (Ryan 1977). Uchida (1936; species recorded as *Konokareha daisetsuzana* Matsumura) found adults present in August at Daisetsu.

Behavior:

Adult male *G. rossii* are diurnally active in alpine habitats, are rapid flyers, and are attracted to females by a pheromone in both the Arctic (Oliver et al. 1964) and on Daisetsu (Kumata 1979). Although Ferguson (1978) states that females do not fly though they have fully-developed wings, this is apparently true only in the Arctic; since Kumata (1979) has observed female flight on Daisetsu. Flight, or at least active movement by females, is also suggested by the locations of egg masses. For example, on Daisetsu (24 IX 76), we found numerous egg masses on upright stems of several woody plants but none on the surfaces of the many cocoons in the same area. Egg masses were frequently found on cocoon surfaces at Devon Island (Ryan 1974). Also the maximum number of eggs in 7 masses at Daisetsu was 124, but the average was only 79. Thus is it likely that the females deposited more than one egg mass. Ryan (1977) recorded a mean of 139 eggs (n = 23) per mass at Devon Island though a single female produced 240 eggs. No eggs were found on Katahdin.

Newly-hatched larvae at Devon Island spun silk and dangled from supporting vegetation (Ryan 1974). When similar larvae from Daisetsu were held in the laboratory, no silk production could be detected, even when we attempted to induce ballooning by blowing larvae off a substrate. Newly-hatched larvae from Maine were not available for similar tests.

On Daisetsu (10 VII 78), only one intermediate-stage instar could be found, and this one was well concealed at the base of matted alpine vegetation. It was not visible unless one parted the vegetation. This larva was removed and placed on the surface of the vegetation in full sunshine at midday. It immediately crawled downward to a resting position similar to that from which it had been removed. This was done repeatedly with the same results. Then the larva was placed on vegetation completely shaded by an embankment. It remained there for over 15 minutes. Temperatures were not recorded but it was evident that solar warming of the larva resulted in evasive behavior. Perhaps during summer days, temperatures can exceed an undetermined threshold above which larvae seek a cooler niche and become inactive. Such intolerance and avoidance of certain warm temperatures, may explain why no other larvae were found on this particular trip.

On another trip to Daisetsu (17 IX 75), mature larvae were numerous and active during midday when the temperature was 11°C. Many were seen walking over stones or barren ground and were actively feeding on suitable vegetation. Possibly in an alpine habitat where winter comes early, midday hours provide the only temperatures suitable for activity. At night (at ca 6000 ft elevation in Hokkaido), freezing conditions occur in September.

On Katahdin (14 IX 74), late-stage larvae were seen feeding and moving over the vegetation at temperatures ranging from 5.7 to 7.5°C.

Natural Enemies:

At Katahdin on 20 VII 74, we found 4 estimated 3rd-instar *G. rossii*. One day later, a larva of *Nepiera* sp.[3] (Hymenoptera: Ichneumonidae) emerged from one of the moth larva and pupated. The adult parasitoid subsequently developed but died while attempting to emerge from its cocoon. Also larvae collected 14 IX 74 at Katahdin produced several puparia that eventually emerged as adult *Spoggosia*

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[3] Identified by R. C. Carlson, SEL, IIBIII, AR, SEA, USDA, Beltsville, MD 20705.

gelida (Coquillet)[4] (Diptera: Tachinidae). This represents a new North American distribution record for this species outside of the high Arctic. These maggots emerged from mature moth larvae or pre-pupae already within a cocoon and at least 3 puparia were recorded from a single host. Later when we dissected 8 nearly mature *G. rossii* that lived in the laboratory to 8 III 75, we found 6 presumed *S. gelida* maggots (2 each in 3 hosts). The maggots were small (mean 2.2 X 1.3 mm), distributed evenly from the mesothorax to the 8th abdominal segment, and positioned internally just beneath the dorsal integument. A small orifice to the respiratory funnel was visible externally when setae were removed.

On Daisetsu, 17 IX 75, the larval population showed definite signs of a viral disease epizootic. Dead larvae placed in a vial disintegrated and a whitish precipitate characteristic of virus was present. It was not determined whether this virus was a NPV or CPV. Also when many cocoons collected on the same date were opened, 12.8% of 78 pupae had been killed by a pupal parasite thought to be a large ichneumonid similar in habits to *Coccygomimus* spp. based on the emergence hole. No specimens have yet been obtained.

Evidence of predation on *G. rossii* was found when we examined the stomach contents of a shrew (*Sorex* sp.) found dead on Daisetsu 24 IX 76. The stomach contained pieces of larvae (prolegs, integument, and setae) of *G. rossii.*

Populations:

Little information is available concerning *G. rossii* populations because of the inaccessibility of its natural habitats. Also, when one hikes through these mountainous areas, only scattered individual insects are usually seen. However, at one time on Katahdin (14 IX 74), mature larvae were so numerous they were often trampled as hikers moved along the hiking trail. It was at this time that we collected 26 larvae for rearing to assess parasite levels. Of these, 19 pupated, 12 adult *G. rossii* emerged, and 11 *S. gelida* emerged from those that did not pupate. The 7 larvae that died were dissected, examined internally, and several more maggots, presumed to be this same tachinid, were found. Thus *S. gelida* caused significant mortality. Ryan (1977) found *Gynaephora* cocoons (he did not distinguish between 2 species) to be 17% parasitized, with a mean of 4 flies/host.

Gynaephora rossii were rather plentiful on Katahdin in 1974. However, the junior author made 5 ascents during the 1975 season (24 V, 19 VI, 7, 17, 28 VIII) and found only one live pupa (19 VI). This scarcity reflects the unpredictability of populations from one season to the next and may indicate a cyclic appearance of any given life stage because of the extended period of larval development.

Meanwhile, on Daisetsu (17 IX 75), larvae were quite abundant in areas with sufficient vegetation. One 3 x 8-m plot had at least 150 larvae, many actively feeding. This density was sufficient to cause nearly complete defoliation of plants within this limited area, especially *R. aureum*. Subsequent observations at the same site indicated that this was not a common occurrence, which again suggests that populations fluctuate dramatically and may even be cyclic, not infrequent for many lymantriid species. The result of the observed outbreak in 1975 in this delicate alpine habitat was that in 1976 and 1978. the *R. aureum* plants were in poor condition. Some plants had sparse foliage, and others were dead. Probably it will

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[4] Identified by C. W. Sabrosky, SEL, IIBIII, AR, SEA, USDA, Beltsville, MD 20705.

take many years for this particular vegetation to completely recover from the effects of defoliation by *G. rossii.*

Notes from Field-Collected Material:

A total of 26 larvae obtained at Katahdin on 14 IX 74 were returned to the laboratory for rearing. The mean live weight of these larvae was 0.389 g. In the laboratory, the larvae were divided into 6 groups (held at 5, 15, or 23°C in a 16L:8D photoperiod or in complete darkness). At 5°C no feeding occurred on *S. babylonica* or *P. fruticosa* leaves, and photoperiod had no apparent effect. Generally larvae were inactive, though they moved slightly. When these same larvae were warmed to 15°C on 25 XI, they spun silk cocoons. They were moved to 23°C on 2 XII. The 5°C temperature apparently prohibited silk spinning but did not completely stop movement though the temperature was probably close to a lower threshold for activity.

Larvae initially held at 15°C (from 18 XI to 4 XII) fed only slightly (measured by frass production), but silk spinning was evident in a number of dishes. This production of silk did not take place during normal feeding; it commenced just before molting to the pre-pupal stage. On 4 XII these larvae were moved to 23°C, feeding was more evident, and cocoon formation began 18 XI. By 1 XII, one female *G. rossii* emerged before 19 XII and 5 *S. gelida* adults emerged from 2 to 13 XII. Duration of the pupal stage at 23°C required 14 days for 2 moths and 8-10 days for the *S. gelida.*

It is significant that development of *G. rossii* continued uninterrupted after the September collection even though 23°C is not typical of ambient temperatures of the normal environment. Oliver et al. (1964) suggested that obligatory diapause probably occurred during the final instar, but our experience suggests that this is not true. Apparently, development may continue throughout any larval instar so long as temperatures (and probably photoperiod) remain favorable for development. In fact, on Daisetsu we recorded active feeding at 11°C and on Katahdin at 5.7 to 7.5°C.

One pupa collected on Katahdin 19 VI 75 emerged in the laboratory on 23 VI and produced some infertile eggs 2 days later. This seems to indicate that at Katahdin, adult emergence would occur in late June and likely July. Ferguson (1978) gives emergence dates 4 to 28 VII for adults collected in the southern alpine habitats.

Biological Comparisons:

Subtle differences were apparent among these widely separated *G. rossii* populations. Larvae at Katahdin were a more slate-colored gray than the more nearly brownish-gray larvae from Daisetsu. Also Ryan (1974b) noted that mature larvae forwarded to him from Katahdin had a different appearance than those from Devon Island and were smaller than mature Arctic larvae. For example, in a collection of 156 larvae of *Gynaephora* spp. (may include *G. groenlandica* (Homeyer), Ryan (1977) recorded a mean live weight of 630 mg; a similar figure for 20 larvae collected 13 IX 74 at Katahdin was 390 mg. Larvae from Daisetsu were not weighed but appeared to closely approximate those for Katahdin. In addition, coloration of some of the secondary setae on the thoracic tufts differed noticeably. Ferguson (1978) described these setae as "bright sulphur yellow". These same setae on living larvae from Katahdin were lemon yellow and on Daisetsu more reddish-orange. Ryan (1974b) noted similar distinctions between Katahdin and Devon Island larvae and stated that the latter were more orange. Elsewhere Ryan

(1974a) stated that Arctic specimens were black and orange as Curtis (cited in Scudder et al. 1879) had first recorded.

Adult *G. rossii* were compared by H. Inoue (1978) in an effort to clarify similarities between *G. rossii* and *G. lugens* Kozhanchikov. He found slight differences when he compared a valve from the genitalia of a male from Katahdin with ones from Daisetsu, but he examined too few specimens to reach a definitive conclusion. Ferguson (1978) concluded that *G. lugens* was a synonym of *G. rossii*, and he noted marked geographical variation among arctic specimens. This morphological variation is apparently even more pronounced when one is comparing individual insects from wider geographical locations.

There were other differences between the Arctic and alpine populations as summarized in Table 2. Foodplants for the alpine populations were species in the Ericaceae; plants in the Rosaceae and *Salix* are reportedly utilized in the Arctic (Ryan 1974; Ferguson 1978; Scudder et al. 1879). Also females appear to have evolved different oviposition behaviors: in the Arctic, they deposit many eggs on the surface of the cocoons from which they emerge (Packard 1877; Ryan 1974). At Daisetsu, eggs were positioned almost without exception on low upright twigs (often dead) of woody shrubs (Table 1 gives species) and not directly on or associated with cocoons, which were found lower in the vegetation mat at the same site. The masses were in irregular naked clusters often completely surrounding the stem and sometimes 3-4 layers deep.

It is not surprising that there are numerous differences among populations of the same species over widely divergent geographical locations (Maine, Hokkaido, and the Canadian Arctic), though all have similar extremes in environmental conditions. Probably spatial isolation of the 2 relict populations and the Arctic population has allowed evolution to work independently since the last glacial retreat. It is only a matter of time until genetic drift will have progressed to such a degree (if it has not already done so), that these populations would no longer interbreed if they were ever reunited.

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Table 2

Synopsis of differences (morphological, behavioral, and recorded natural enemies) among 2 alpine relict populations and the Arctic populations of *Gynaephora rossii*

		Mt. Katahdin, Maine U.S.A.	Mt. Daisetsu, Hokkaido, Japan	Canadian & Alaskan High Arctic
Coloration of mature larvae:	Overall:	Slate-Gray	Brownish-Gray	Black[a,b]
	Shorter dorsal-lateral setae:	Lemon-Yellow	Reddish-Orange	Orange[a,b]
Oviposition Sites:		Unknown	Upright Woody Stems	Cocoon Exterior[c]
Food Plant Genera:		*Vaccinium*	*Rhododendron*	*Saxifraga*[d]
		Potentilla	*Phyllococe*	*Salix*[d]
			Geum	*Dryas*[d]
Natural Enemies:	Parasites*	*Spoggosia gelida* (L)	Ichneumonid sp. (P)**	*Spoggosia gelida* (L)[b]
		Nepiera sp. (Early L)		*Rogas* sp. (L)[b]
				Pterocormus byrdiae (P)[e]
	Predators:		*Sorex* sp.	
	Diseases:		Virus	
Source/Reference:		Present Study	Present Study	[a] Scudder et al 1879 citing Curtis [b] Ryan 1974, 1977 [c] Packard 1877 [d] Ferguson 1978 citing others [e] Krombein et al 1979 citing Heinrich 1956

* Letter designates host stage attacked, L-larvae, P-pupae. ** Based only on evidence of pupal remains since a *Coccygomimus*-like parasite had emerged from 12% of *G. rossii* pupae but no specimens were observed.

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On the Evolutionary Distance Between Asclepiadaceous-Feeding Danaida and Apocynaceous-Feeding Ithomiids

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The purpose of this brief communique is to report on some preliminary larval feeding tests in which larvae of the Monarch Butterfly *Danaus plexippus* were offered the larval host plant of the ithomiid *Tithorea pinthias*, a species from the tropical wet forests of Costa Rica. *Tithorea* larvae were also offered the host plant of *D. plexippus*. Since *D. plexippus* utilizes various species of *Asclepias* in the Asclepiadaceae as larval host plants, and *T. pinthias* larvae normally feed on *Prestonia* and other apocyanaceous plants, and because the Danaidae and Ithomiidae are considered to be closely related families (Ehrlich and Raven 1965 and others), these "reciprocal-exchange" feeding tests were conducted to determine whether or not each butterfly species could survive on the other's host plants. Stated somewhat differently, the ability of larvae to feed on interchanged host plants is in part a function of the degree of evolutionary divergence between danaids and ithomiids in terms of those physiological traits regulating feeding abilities. The assumption is made that *D. plexippus* is a generalized danaid phenotype while *T. pinthias* is a generalized apocanaceous-feeding phenotype, the latter distinction being made since most ithomiids are solanaceous-feeders (Ehrlich and Raven 1965). The rationale of the tests conducted as described below incorporates a check for the ability of *T. pinthias* to feed on a cultivated solanaceous plant species.

Tithorea pinthias larvae, from the time of hatching, were exposed to *Prestonia* and *Asclepias* separately, and in a choice situation in which these plants and tomato were present together. Three larvae, all from eggs from one female in Costa Rica, were used. Using four larvae in each test *D. plexippus* Linnaeus was examined on a wild host plant, *Asclepias syriaca, Prestonia* sp., and tomato. The *Prestonia* came from a greenhouse culture at the Milwaukee Public Museum established in 1975 from material brought from Costa Rica. In all tests the eggs were introduced along with fresh cuttings of the host plant into a clear plastic bag. All six bags were kept in the same laboratory and under the same conditions (usually 24 degrees C at 1200 hours and 50% r.h.). When the eggs hatched, the contents of each bag were examined daily to check for feeding (leaf damage and presence of fresh fecal material) and larval survival. The experiment lasted as long as there were surviving larvae in the bags.

All of the *T. pinthias* larvae reared on *Prestonia* survived to adulthood as did all *D. plexippus* larvae reared on *Asclepias. Tithorea pinthias* larvae give *Asclepias* alone all died in the first instar and larvae completely ignored tomato in the choice test. *T. pinthias* larvae did not feed on *Asclepias.* All *D. plexippus* larvae given *Prestonia* died by the end of the third instar. *Danaus plexippus* larvae fed on *Prestonia,* but in the choice test fed only on *Asclepias.* The *D. plexippus* larvae that survived through the third instar on *Prestonia* were about two-thirds the size of the *Asclepias*-reared larvae in the same instar.

Although the results point to some interesting differences in response patterns by the larvae of each butterfly species to exotic plant species, sample sizes are very small. Given the relatively low population densities and patchy distributions of *T. pinthias* populations in Costa Rica (Young, unpubl. data), it is usually difficult to obtain large samples of eggs. In the discussion that follows, I assume that the patterns observed within the small samples would have also been found in large samples as well, although such effects warrant further study in carefully designed experiments with adequate replication of the tests.

The results suggests that each butterfly species is specialized to some degree in its natural host plant. Of particular interest, however, is the apparent ability of *D. plexippus* larvae to feed on an apocynaceous plant while *T. pinthias* cannot feed on an asclepiadaceous plant. Selectionhas possibly made *T. pinthias* more specialized as an herbivore of Apocynaceae than *D. plexippus* as an herbivore of Asclepiadaceae. The mechanism of selection, of course, implies a genetic adaptation to exploit a particular plant species. An alternative explanation would be that *D. plexippus* is more phenotypically flexible to process foodstuffs and associated plant products from the two plant families, perhaps the result of mixed physiological mechanisms present (Young 1980). Heywood (1978) has stressed the close affinities between the Asclepiadaceae and Apocyananaceae. But such flexibility has limits: while some danaids may feed interchangeably on Asclepiadaceae and Apocynaceae (Ehrlich and Raven 1965), *D. plexippus* feeds successfully (i.e., to pupation) only on Asclepiadaceae.

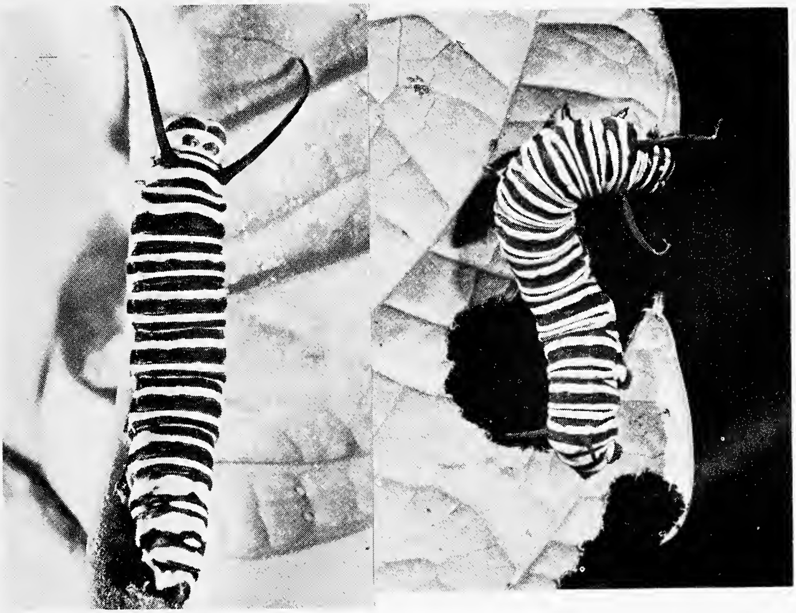

Fig. 1. Left: third instar larva of *Tithorea pinthias* (Godman & Salvin) on *Prestonia* sp. (Apocynaceae).
Right: third instar larva of *Danaus plexippus* Linnaeus feeding on *Prestonia*. Note the defoliated portions of the leaf resulting from feeding by *D. plexippus*. The larvae of both butterflies possess mesothoracic tubercles and similar color patterns.

D. plexippus possesses chemo-behavioral sensory mechanisms for tasting and ingesting both host plant families, but the eventual death of the larvae on *Prestonia* suggests an inability to completely digest tissues or sequester toxic secondary compounds from this plant. Although Klots (1951), mentions that *D. plexippus* feeds on both Asclepiadaceae and Solanaceae, the danaids as a group are well known for exploiting Asclepiadaceae and Apocynaceae, especially the cardonolide-containing sections of these groups (Ehrlich and Raven 1965, Duffey and Scudder 1972, Edgar *et al.* 1974). The Ithomiidae exploit both Solanaceae and Apocynaceae (Brower and Brower 1964; Erhlich and Raven 1965) and the results presented here for *T. pinthias* suggests that the Ithomiids consist of two sections, specialized for exploiting the two plant groups, and that interchangeable feeding probably does not occur.

If the apocynaceous-feeding habit is a primitive condition in both the danaids and ithomiids, *D. plexippus* still possesses the ability to penetrate this plant family, even if only partially successful. The trait has not been completely lost in at least one asclepiadaceous-feeding danaid. The genes regulating olfactory acuity and other aspects of the host plant location behavior for Apocynaceae have not been entirely lost from the gene pool. On the other hand, the apparently complete inability of apocynaceous-feeding ithomiids such as *Tithorea*, and perhaps *Aeria* (Young 1978), to feed on Asclepiadaceae suggests that these butterflies did not have evolutionary contact with this group, or were not preadapted to penetrate the plant family as a new ecological resource. Similarly both *Danaus* and *Tithorea* had no evolutionary contact with the Solanaceae and neither butterfly is preadapted to utilize this plant group. Although it is maintained that the Asclepiadaceae and Apocynaceae are very closely related in terms of many characteristics including secondary compound chemistry (Safwat 1962; Alston and Turner 1963), a portion of the phenotypic characteristics of each plant group creates unique spheres of selection pressures resulting in partial or total host plant specialization for danaids and ithomiids.

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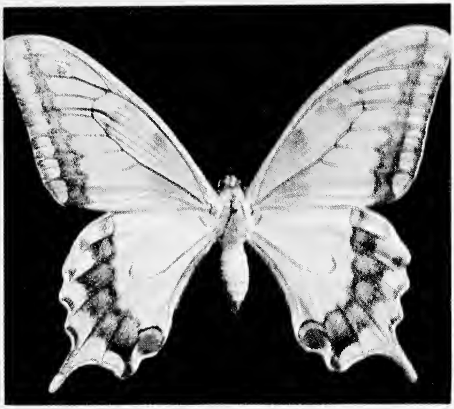

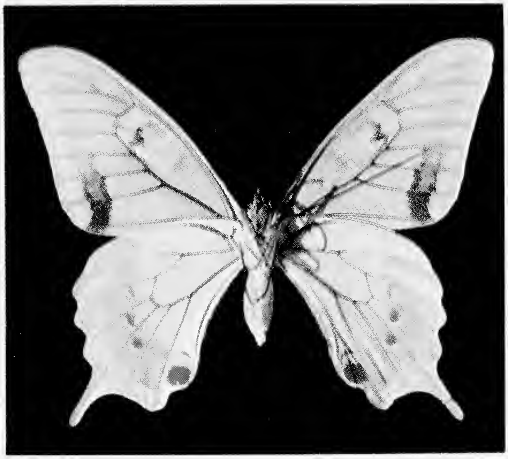

An Aberrant Oregon Swallowtail, *Papilio oregonius* Edwards from Oregon

On 28 August 1967 an apparently unique aberration of a female Oregon swallowtail, *Papilio oregonius* Edwards emerged in the entomology laboratory of the Oregon Department of Agriculture, Salem. It was one of six (the other five normal) reared from larvae collected on *Artemesia dracunculus* L., 5 miles East of The Dalles, Wasco Co., Oregon, by Kenneth Goeden. The wingspread is 85 mm, body length 26 mm. The aberration exhibits an extreme reduction in melanic scales, which are strongly suffused with yellow ones. The condition is more pronounced ventrally and melanic scales are entirely absent on the body. In *P. oregonius* I am not aware of another aberration of any kind, let alone one of such a striking nature.

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The Scolitantidini II. The World's Smallest Butterfly? Notes on *Turanana*, and a New Genus and Species from Afghanistan (Lycaenidae)

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In the course of studying the paleartic components of the Scolitantidini, the relationship of the genus *Turanana* to other genera within the tribe as well as of its species to one another appeared immediately complex. There is very limited material available for the genus and a substantial amount of field work will be required to provide insights on the group. Single specimens of a related but quite unusual member of this group were seen at both the British Museum (NH) and the Zoologische Sammlung des Bayerischen Staats. Subsequently, I obtained four additional specimens through the courtesy of S. Sakai.

These represent a unique species best placed in a new genus closely related to, but clearly separated from *Turanana*. The species should additionally be recognized as among the world's smallest known butterflies, in size being slightly larger than the smallest but larger than the average specimens of *Brephidium exilis* (6-10 mm forewing expanse, average about 8.5 mm, LACM, 50 specimens). In the matter of size this further exaggerates the extremes in the tribe Scolitantidini from wing expanses of 7 mm in the new entity to 24 mm in *Maculinea arionides*.

Micropsyche Mattoni **new genus.**

Type Species: *Micropsyche ariana*, new species.

Very small butterflies, primary wing span about 7 mm. Eyes hairless, palps dimorphic, 3rd segment either equal to or one-half 1st segment. Meso- and metathoracic leg calcaria short and thick and any tibial processes absent. Androconia absent. Prominent forewing UPS discoidal macule prominent, UPF with five macule postmedian constellation prominent with macule M_3 not offset distally UNH with distinct marginal and submarginal macules. Male genitalia: aedeagus without Chapman's process. Valves with crista and articulated to move mesally. Falces heavy proximal half tapering abruptly in distal half. Tegumen shape relatively straight in lateral view of dorso-frontal edge. Saccus absent. Female genitalia: papillae anales subquadrate, posterior apophysis strongly bent. Bursa round. Lamella vaginalis scoop shaped as double laminated troughs. No sexual dimorphism evident.

Not Refereed

Micropsyche ariana Mattoni new species.

Holotype male: Head. eyes fringed white, scales, two rows black scales parallel below antennae. **Eyes.** hairless. **Palps.** (Fig. 3) ratio segments 1:2.6:0.8, white scales above, fuscous below, dense black hair scales dorsally and medially. **Antennae.** white below, white with fuscous scales at joints above.

Thorax. Legs. *proleg* (Fig. 6; Table 1) *Mesothoracic leg* (Fig. 9) covered white hair scales. Distitarsus with single spine. Without endodont lobes. **Tegula.** specimen lost.

Wings. *Expanse* FW 7.1 mm. *Venation* (Fig. 12; Table 1) *UPS*. Ground color medium brown-gray. Faint cyanic overlay blue scales without clear color differentiation. Androconia lacking. *UPF*. Discoidal macule prominent, black, off-white marking basal and distal. Postmedian constellation five black elongate macules extending CU_2 to M_1, haloed with white. Submarginal and marginal macules indistinct but demarked by white in marginal space between them. Fringe white, not checkered. *UPH*. Three postmedian haloed macules in M_1, M_2 & M_3. Weak discoidal macule with faint white borders proximal and distal. Marginal markings as UPF. *UNS*. Ground light brown, slightly darker in basal quarter. *UNF*. Maculation as UPF, except macules more prominent on lighter ground. Submarginal macules distinct, punctuated by white, marginal band distinct. *UNH*. Distinct discoidal macule. Postmedian macules from 1A through R. Haloed as UNF. Submarginal and marginal markings as UPF.

Genitalia. (Figs. 14, 15, 28, 29) As under generic description. Aedeagus with two sets of cornuti. Weakly bi-lobed.

Allotype Female: Features as above, no evidence of sexual dimorphism in any characters except genitalia. **Genitalia.** (Fig. 33) As in generic description.

Variation. The most striking variation appears in the dimorphism of the palps (Fig. 3 A & B). In the type series of five specimens, 3 males have palps of type A, one male and the single female type B. In wing pattern, there is minor variation in depth of the UPS ground, the number of postmedian macules of both UPH and UNH, and presence or absence of the UNS marginal macules. There are insufficient specimens to reliably document variation.

Type Data. Holotype and male paratype 1, Afghanistan, Mt. Khwajaghar, Koh-i-Baba Mts., 3600-4000 meters, 2 VII 75, allotype and male paratype 2, same locality, 3 VII 75, leg. T. Shimizu. Paratype 3, male, same locality, 17 VI 73, no leg. data (BMNH colln.).

Type Disposition. Holotype and allotype will be placed in the BMNH with paratype 3. Paratypes 2 and 3 are property of S. Sakai.

Biology. There are no data.

Diagnosis. By virtue of gross conformation of the male genitalia, *M. ariana* clearly is in the tribe Scolitantidini. Comparative morphological features, including palps, legs, and genitalia are illustrated in Figs. 3-36, and major differentiating characters are summarized in Table 1. The genus, which is monotypic, would appear most closely related to *Turanana*, a genus comprised of at least six species and *Glaucopsyche*, conservatively comprised of at least eight species. With regard to major characters of the legs: ratio of segments, tibial process, calcaria, and

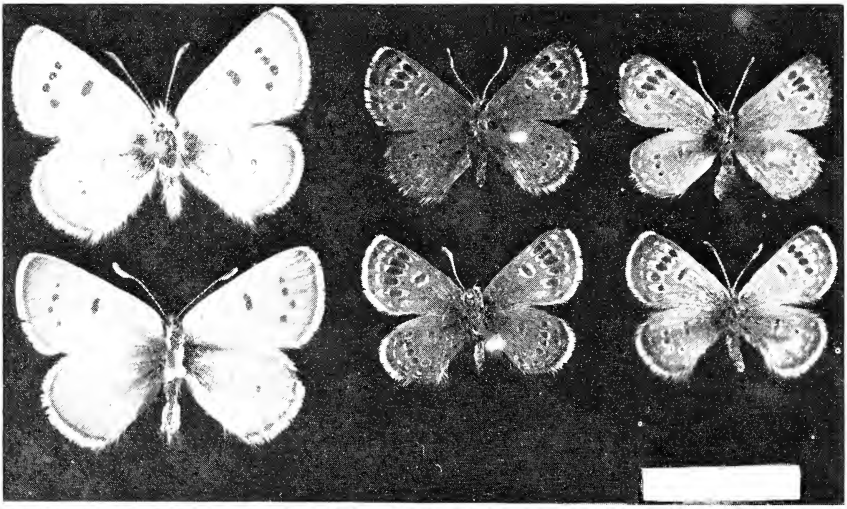
Table 1

Comparison of *Micropsyche, Turanana* and *Glaucopsyche* based on morphological characters and major wing pattern elements which are variable within the related group.

Character	*Micropsyche ariana*	*Turanana cytis*	*Turanana panagaea*	*Glaucopsyche alexis*	*Glaucopsyche lygdamus*	*Glaucopsyche melanops*
[1]Eye Hairs	0	1	2	3	3	3
Mesothoracic, leg, dorsal tibial process	0	0	0	+	+	+
[2]Mesothoracic, leg, calcaria shape	1	2	2	3	3	3
Venation:						
A:B	1.11:	1.00:	0.81:	1.00:	0.90:	0.93:
B:C	2.00	1.62	1.50	1.86	2.00	1.67
UPF, discoidal macule (♂)	+	+	+	0	0	0
UPF, postmedian constellation	+	+	0	0	0	0
UNH, marginal macules	+	+	+	0	0	+
UNF, M^3 postmedian macule offset proximally	0	+	+	0	0	0
Androconia	0	0	0	+	+	+
Aedeagus--Chapman's process	0	0	0	+	+	+
Valves--Crista	+	0	0	0	0	0
[3]Valves--Articulation	L	L	L	D	D	D
[4]Falces	C	F	F	B	B	B
[5]Tegumen shape lateral aspect	S	S	S	H	H	H
Saccus	M	+	+	+	+	+
[6]Bursa shape	R	E	E	E	E	E
[7]Papillia anales	S	S	S	T	T	T
[7]Papillia anales shape	S	S	S	T	T	T
[8]Lamella vaginalis	D	B	B	S	S	S

Legend: + = present; 0 = absent; M = minute; [1]Eye Hairs: 0 = none; 1, few >0.1 mm; 2, few <0.05 mm; 3, many >0.1 mm; [2]Calcaria: 1 = short, thick; 2 = long, thin; 3 = long, thick; [3]Valves: L = lateral; D = dorso-ventral; [4]Falces: C = thick basal, fine proximal; F = thin, long; B = heavy; [5]S = approximately straight dorso-frontal shape (lateral view); H = as before, humped; P = strongly humped; [6]R = round; E = elongate; [7]S =subquadrate; T = elongate subtriangular; [8]S = shovel shape; B = bowl shape; D = deep scoop shape chaetotaxy, the intragenetic variation is minimal while the differences between genera are constant. Distitarsus chaetotaxy (Figs. 9 & 10) is consistent for both *Glaucopsyche* and *Turanana*. *M. ariana* alone has no eye hairs. *M. ariana* shares with all *Turanana* lack of androconia. In the male genitalia, *M. ariana* has a unique falx conformation, but shares a similar shape of the tegumen with *Turanana*. The aedeagus of *M. ariana* and *Turanana* (all species observed) are similar, lacking Chapman's process, so evident in *Glaucopsyche*. What may be a major feature in functional similarity within *M. ariana* and *Turanana* is the valve hinging or articulation. In these genera the valves move predominantly mesally in comparison with *Glaucopsyche* where the movement is dorsal. The matter is exemplified in the lateral views of the genitalia (Figs. 15-21). Shape of the valves themselves appears to be of use only as a specific character (Figs. 22-27). The substantial variation within *Turanana* is only partially illustrated (see also Fig. 18) in that subspecific variation in the character emerged at least in the case of *T. panagaea* from Turkey and Iran. Beuret (1959. Mitt. Basel Ent. GES 9: 80-84), placing major weight on valve shape went so far as to suggest *T. panagaea* is related to *Actizera* and *T. cytis* to *Philotes sonorensis*. The assertion was without merit. *M. ariana* is unique in the group in that its valves have a crista. In the female genitalia the shape of the papillae anales are subquadrate in *M. ariana* and *Turanana*, compared with a subtriangular shape in *Glaucopsyche*. In *Turanana* there is considerable variation in the structure (see Fig. 36 A, *T. panagaea*) which is not evident in *Glaucopsyche*. Lastly, the formationof the lamella vaginalis in *M. ariana*, as two curved sclerotized curved plates (Fig. 33 B & C) and the round bursa copulatrix are unique, although the lamella more closely resembles *Turanana* species than those of *Glaucopsyche*. On these bases, I intuitively believe *Micropsyche* is a unique group, most closely related to *Turanana*.

Acknowledgements: Particular thanks to Richard Vane-Wright of the British Museum (N.H.) for generously providing specimens and work space; W. Forster and W. Dierl of the Zoologische Staats Sammlung, Munchen for the same courtesies, Anttl Aalto, Finland for specimens, Willem Blom, Netherlands for specimens and Seiji Sakia, Japan for specimens.



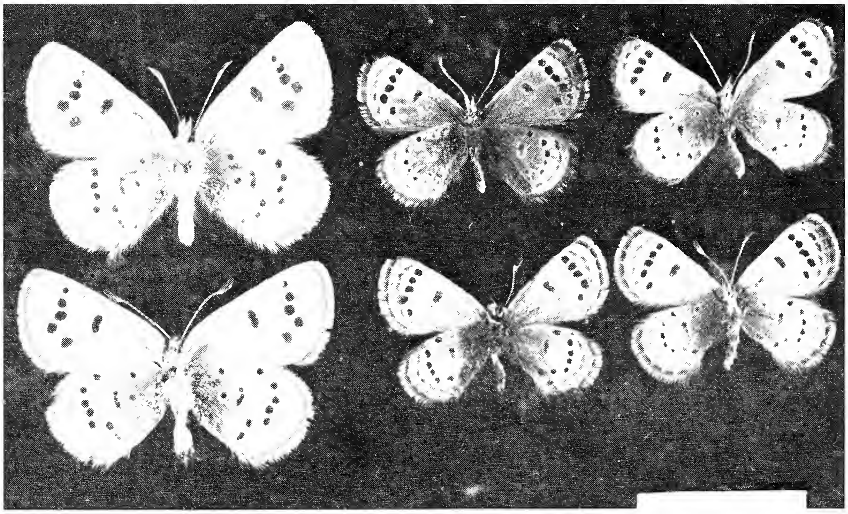
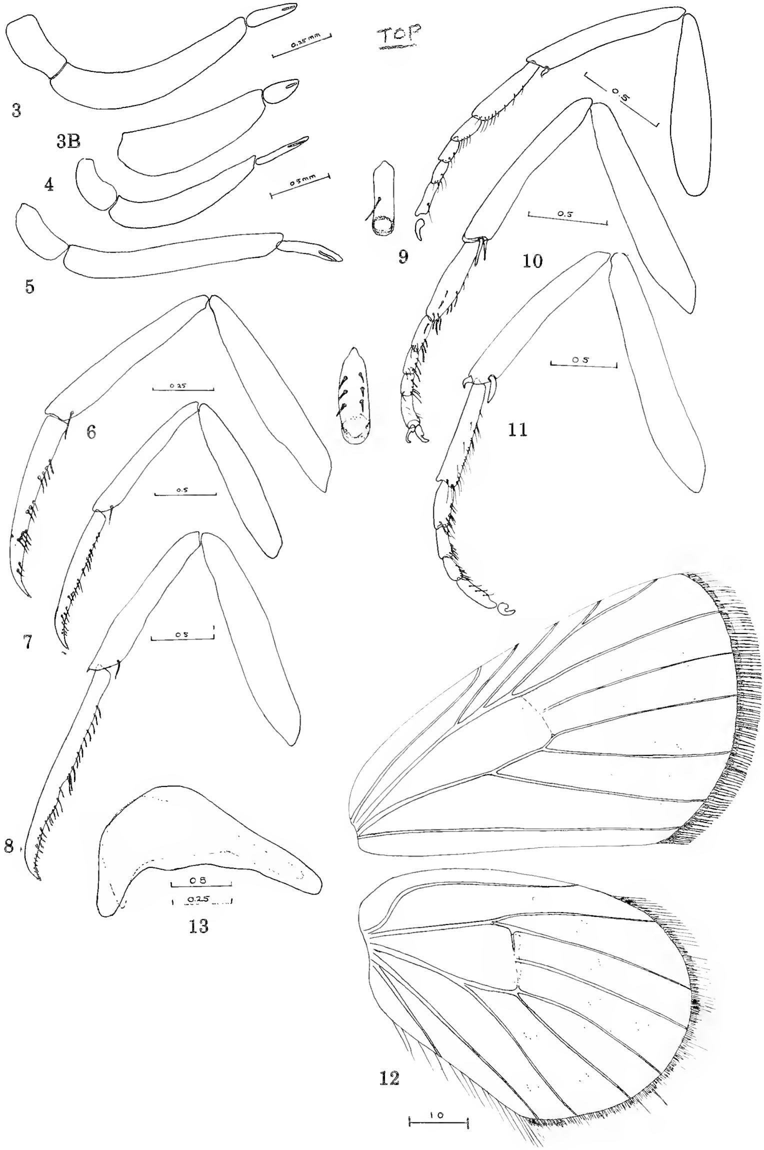


Fig. 1. 1st Col. *Turanana cytis* male above, female below, Iran: Kudara, 17 VI 1887, Gr. Gr. (BMNH); 2nd Col. *Micropsyche ariana* male paratype 1 above, 2 below; 3rd Col. same holotype male above, female below. Specimens enlarged about 2X. Mark = 1.0 cm.

Fig. 2. Undersides of Fig. 1.

Fig. 3. Palp *M. ariana*, A) male para. 3, B) male para. 2.
Fig. 4. Palp *T. panagaea*, male, Turkey, RHTM 152.
Fig. 5. Palp *G. alexis*, male, Finland, RHTM 169.
Fig. 6. Male prothoracic leg. *M. ariana* para. 2.
Fig. 7. Ibid. *T. panagaea*, RHTM 157.
Fig. 8. Ibid. *G. alexis*. RHTM 170.
Fig. 9. Male mesothoracic leg. *M. ariana*, showing chaetotaxy of disti-tarsus para. 2.
Fig. 10. Ibid. *T. panageae*, RHTM 174, showing chaetotaxy of disti-tarsus.
Fig. 11. Ibid. *G. melanops*, RHTM 138, showing chaetotaxy of disti-tarsus.
Fig. 12. Wing venation, *M. ariana*, male holotype.
Fig. 13. Tegula, *T. cytis* (dotted line), *G. alexis* (solid line).
Fig. 14. Male genitalia, caudal view, *M. ariana* para. 2.
Fig. 15. Male genitalia, lateral view, *M. ariana*, para. 2.
Fig. 16. Ibid. *T. cytis*, RHTM 89.
Fig. 17. Ibid. *T. panagaeides*, RHTM 112.
Fig. 18. Ibid. *T. anisopthalma*, RHTM 111.
Fig. 19. Ibid. *G. alexis*, RHTM 170.
Fig. 20. Ibid. *G. lygdamus*, RHTM 76-11.
Fig. 21. Ibid. *G. melanops*, RHTM 67.
Fig. 22. Right valve, caudal view, flattened, *M. ariana*.
Fig. 23. Ibid. *T. panagaeides*, RHTM 159.
Fig. 24. Ibid. *T. panagaea*, RHTM 158.
Fig. 25. Ibid. *T. cytis*, RHTM 89.
Fig. 26. Ibid. *G. alexis*, RHTM 169.
Fig. 27. Ibid. *G. melanops*, RHTM 137.
Fig. 28. Aedeagus, ventral view, *M. ariana*.
Fig. 29. Aedeagus, lateral view, *M. ariana*.
Fig. 30. Ibid. *T. panagaeides*, RHTM 159.
Fig. 31. Ibid. *G. alexis*, RHTM 169.
Fig. 32. Aedeagus, lateral view, *G. alexis*, RHTM 169.
Fig. 33. A) Papilla anale & anterior apophysis, B) Lamella vaginalis, lateral view & C) Lamella vaginalis, ventral view, *M. ariana* allotype.
Fig. 34. Ibid. *G. alexis*, RHTM 178.
Fig. 35. Ibid. *G. melanops*, RHTM 180.
Fig. 36. Ibid. *T. panagaea*, papilla anales of 3 specimens shown for variation, A_1, A_2, A_3.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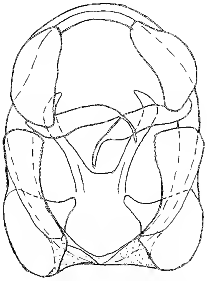

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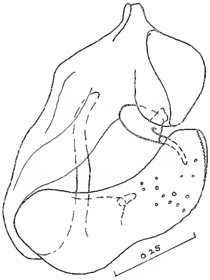

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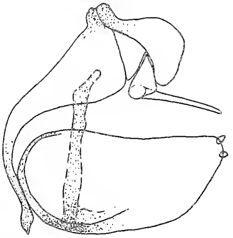

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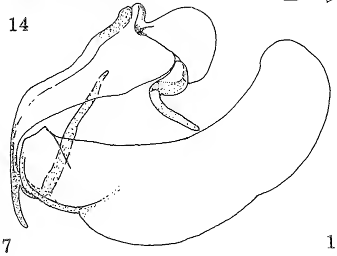

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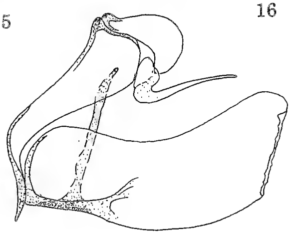

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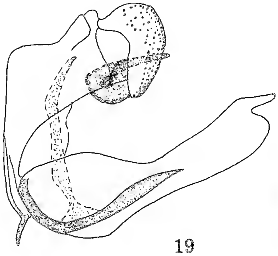

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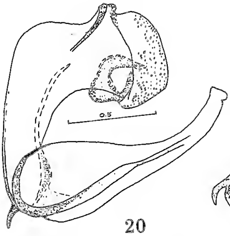

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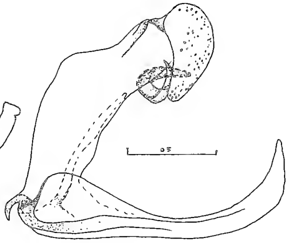

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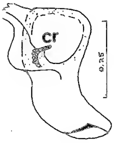

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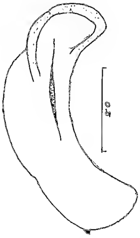

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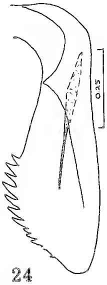

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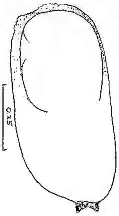

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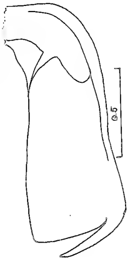

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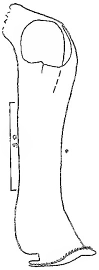

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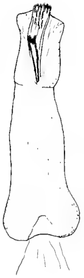

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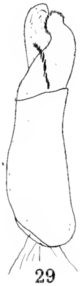

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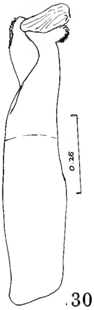

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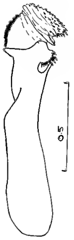

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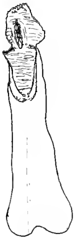

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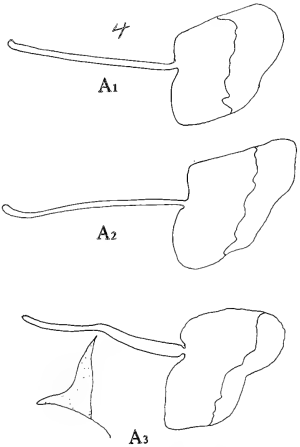

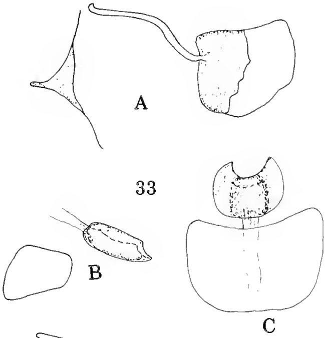

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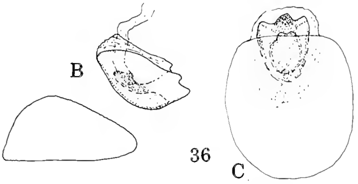

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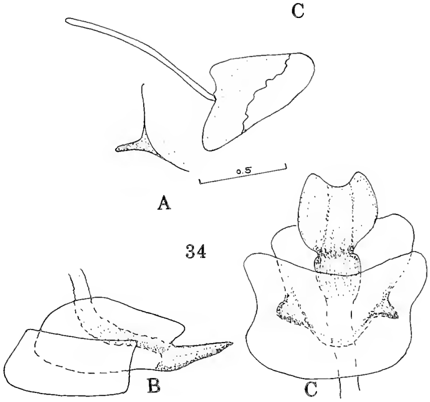

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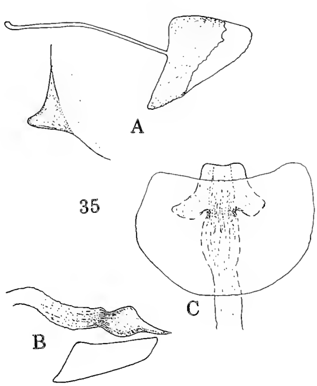

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INSTRUCTIONS TO AUTHORS

Manuscript Format: Two copies *must* be submitted (xeroxed or carbon papered), double-spaced, .typed, on 8½ x 11 inch paper with wide margins. Number all pages consecutively and put author's name at top right corner of each page. If your typewriter does not have italic type, underline all words where italics are intended. Footnotes, although discouraged, must be typed on a separate sheet. Do not hyphenate words at the right margin. All **measurements** must be metric, with the exception of altitudes and distances which should include metric equivalents in parenthesis. **Time** must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. **Dates** should be cited as example: 4. IV. 1979 (day-arabic numberal; month-Roman numeral; year-arabic numeral). Numerals must be used before measurements (5mm) or otherwise up to number ten e.g. (nine butterflies, 12 moths).

Title Page: All papers must have the title , author's name, author's address, and any titular reference and institutional approval reference, all on a separate title page. A **family citation must** be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding two typed pages must be accompanied by an abstract of no more than 300 words. An additional summary is not required.

Name Citations and Systematic Works: The first mention of any organism should include the full scientific name with author (not abbreviated) and year of description. New descriptions should conform to the format: male: female, type data, diagnosis, distribution, discussion. There **must** be conformity to the current International Code of Zoological Nomenclature. We strongly urge deposition of types in major museums, all type depositions must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbrevations must conform to the *World List of Scientific Periodicals.* Do not underline periodicals. If four or less references are cited, please cite in body of text not in Literature Cited.

Tables: Tables should be minimized. Where used, they should be formulated to a size which will reduce to 4 x 6½ inches. Each table should be prepared as a line drawing or typed with heading and explanation on top and footnotes below. Number with Arabic numerals. Both horizontal and vertical rules may be indicated. Complex tables may be reproduced from typescript.

Illustrations: Color must be submitted as a transparency (i.e., slide) ONLY, the quality of which is critical. On request, the editor will supply separate detailed instructions for making the most suitable photographic ilustrations. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors **must** plan on illustrations for reduction to the 4 x 6½" page. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink at least twice the final size. Include a metric scale or calculate and state the actual magnification of each illustration as printed. Each figure should be cited and explained as such. The term "plate" should not be used. Each illustration should be identified as to author and title on the back, and should indicate whether the illustration be returned.

Legends should be separately typed on pages entitled "Explanation of Figures". Number legends consecutively with separate paragraph for each page of illustrations. Do not attach to illustrations. Retain original illustrations until paper finally accepted.

Review: All papers will be read by the editor(s) & submitted for formal review to two referees. Authors are welcome to suggest reviewers, and if received, submit name & comments of reviewers.

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Volume 18 *Number 4* *Winter, 1979(81)*

IN THIS ISSUE

Date of Publication: April 24, 1981

COVER ILLUSTRATION: *Danaus plexippus*, third instar larva, feeding on *Prestonia*. Young, pages 251-254.

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WILLIAM HOVANITZ, 1915-1977
MEMORIAL ISSUE

Volume 17 *Supplement* *1978(79)*

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Journal of Research on the Lepidoptera 17 (Supplement): 1-6, 1978(79)

DR. WILLIAM HOVANITZ, 1915 - 1977

RUDOLF H. T. MATTONI

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Bill Hovanitz died suddenly of coronary failure early Wednesday morning, September 14, 1977. He left us quickly, without pain, and quite prematurely. He left many of us with a large sense of loss, which to me was deeply personal as well as scientific. To those who respected his remarkable legacy of work on butterflies, there is a profound sadness that we will never see Bill's interpretation of a large body of data which he was just beginning to organize for publication. A vigorous, involved, intense, efficient, and brilliant individual has left a scene enriched by his all-too-brief appearance upon it.

The life of the man was dialectic rather than following a linear pattern of defined milestones within our system to which most humans become committed. Although Bill's major goal and direction from an early age was understanding the patterns of variation and distribution of butterflies, his curiosity led him to investigate diverse scientific subjects. These interests were superimposed with exigencies of playing the academic game through several institutions, a close family commitment, and his successful ventures into business.

Bill was born in Chicago on November 6, 1915, and was brought to the San Francisco Bay Area of California in 1918, where his interest in nature, especially butterflies, started. To augment family income, as a high school student he was a delivery boy for a San Francisco drug store. While making deliveries about the city he took time to collect specimens, including those used in his early *Plebejus* studies and the now extinct *Glaucopsyche xerces,* on the side. He entered the University of California, Berkeley, in 1934, graduating with a B.S. in Entomology in 1938. Accepted to the graduate program at the California Institute of Technology under Nobel-Laureate Thomas Hunt Morgan, he received his Ph.D. in Genetics in 1943. Morgan having died during Bill's graduate career, he finished under A. H. Sturtevant. Discordance with Sturtevant flavored his subsequent academic pursuits and substantially contributed to the diverse pathways followed. He spent 1942-1945 working for the National Research Council in South America, Michigan and Florida. He then studied with Lee Dice at the Laboratory of Vertebrate Zoology of the University of Michigan, going on to the faculties of Wayne University (Detroit) and University of San Francisco. At the latter, he served as Associate Editor of the *Wasmann Journal of Biology.* He taught summer session at the University of California, Santa Barbara in 1949, where he met and married Barbara. He returned to Cal Tech in 1955, also spending time at UCLA. He finally settled as Professor of Biology at the California State University at Los Angeles in 1956, and resigned from the faculty in 1975. In early 1977 the Hovanitzes moved to Santa Barbara where they planned to build a home and for Bill to devote his full energies to research.

Although Bill's great interest lay in describing and understanding the remarkable patterns of variation within and between populations over distance and time, reflected in the major body of his work, he proposed only four taxa (listed below). His overall philosophy on taxonomy was well expressed in his 1943 paper on *Argynnis callippe* in California. The statement below, taken from that paper, follows a listing of twelve available named entities. Bill then proceeded to list the four major subspecies he recognized and went on to offer a more detailed taxonomy of 9 or 10 subspecies names. After implying that a researcher may choose between these taxonomic approaches as a matter of taste, Bill said:

> Some systematists may feel it desirable to extend further the analysis of the variations by applying names to even more restricted local populations. The author does not think this necessary or desirable, but does consider it of importance that records of variations and distribution be published. The author believes the important part to be the variation and the biological significance of the variation, and this can be studied in any number of ways. For practical purposes of identification in a collection it is desirable that local populations be given names, but variation considered "unnamable" is often as important as, or more important than the latter and should receive its proper place in publications.

In his 1940 paper on an explanation of color variation in *Oeneis chryxus* reprinted in this supplement, the determinants of adaptedness of the subspecies *stanislaus* and *ivallda* are discussed in detail. Thus his earlier description of *stanislaus* (1937) is given significance. The paper on *Plebejus icariodes* (1937), written while a sophomore in college, described the subspecies *missionensis* in terms of its relationship to a Rassenkreis. We see in Bill's early growth as a biologist a view to which we should all be attentive: the importance of interpretation of the significance which underlies the phenomena we perceive, rather than the mere description of the physical manifestations of these phenomena.

In the historical context, Bill produced several outstanding contributions. As a minor note, in his first paper written in 1936 he deplored overzealous collecting and anticipated government protection of endangered species. The paper "Parallel Ecogenotypical Color Variation in Butterflies", reprinted herein, was particularly noteworthy in attempting to demonstrate the existence of complex selective forces of the environment in producing the described color patterns in numerous butterfly species through the diverse regimes of California. This line of work was later beautifully expanded by using examples of *Colias* female dimorphs on a continental scale (1950).

He studied the operation of the complex, often indirect, modes of selection on gene frequency and the partitioning of environmental effects on variation in several taxa, including *Euphydryas chalcedona* (1943, 1952) and *Colias* (1944, 1945). In another classic paper (1948), differences in diurnal activity of orange and white females of *C. eurytheme* were documented in detail and explained in terms of adaptation to diurnally cyclic environmental factors.

Bill was one of the first Lepidopterists to recognize hybridization as a source of variability in butterflies. His first works (1943-1944) on the subject were directed to understanding why hybridization does not swamp the identity of interbreeding species such as *C. eurytheme* and *C. philodice*. His later studies turned to the more significant issue of recognizing hybridization as a major source of variability in populations (1949). He also recognized the concept that hybridization would produce populations adapted to "hybridized" habitats. Thus intermediate hybrid populations would not be selected against in ecological situations intermediate to the environmental modes of the "species" population (1953). A culmination of this work was recognition of *C. boothi* as a hybrid of *C. nastes* and *C. hecla* (1963).

Zoogeography was another aspect of Lepidoptera which fascinated Bill. He synthesized a large amount of data into the first comprehensive review of the subject in 1958, describing the major features of latitudinal and altitudinal distribution of the New World butterflies, except the Hesperiidae.

His most recent published area of work was on food plant preferences, summarized in 1969. The bulk of the research was conducted with graduate student Vincent C.S. Chang and was published in a series of papers between 1962 and 1965 in this journal. Numerous relationships of *Pieris rapae* and *P. protodice* larval food choices and female ovipositional responses on several species of cruciferous food plant were tested. The results are important to all workers concerned with this basic aspect of coevolution.

In addition to work on Lepidoptera, he became quite curious about chromosome ultrastructure and was a pioneer in the attempt to describe such structures through use of the electric microscope in the mid-1940's. Although the techniques were crude by today's standards and conclusions consequently partially questionable, the approach was a decade ahead of its time (1947, 1953, 1956, 1957). Research undertaken for the National Research Council during World War II provided comparative information on adapted responses of mosquitoes with regard to multiple physiological and genetic characters, in part emphasizing parallelism among diverse species (1953, 1957, *et al.*). This work was applied to malaria control. Another fruitful research direction was into the mechanism of insect gall formation in plants. In this work Bill, now the biochemist, and coworkers attempted to isolate the inductive chemicals from insects (1962) and produced a popular review along the way (1959). The gall induction system was viewed as a significant model of certain tumors. In collaboration with Sewall Wright and Dobzhansky (1942) he published a classic study on population structure based on frequency and allelism of lethal genes in *Drosophila pseudoobscura*. Both men had a positive impact on Bill's emphasis on population genetics.

Last but not least, Bill authored a book on general genetics: *Textbook of Genetics* (1953). Designed for beginning classes in Genetics, the emphasis was on population genetics and evolution. The value Bill placed on open and free inquiry is summed in the dedication of his book:

> To the unknown student or students who may be aroused by the unanswered questions herein infused and who may seek out their answers by experiment and synthesis unhampered by transliteral or political expediency.

As a maker of small talk, Bill was a failure. His apparent aloofness and unassuming way to some people was a gentle expression of his impatience with wasteful decorum, pointless conversation, and trivial deeds. I can't help but feel that if Bill were looking over my shoulder now he would be chuckling over my writing his obituary as a rather frivolous undertaking. He was in reality a very warm, positive, and encouraging, yet highly independent individual. His excellence in business matters was a side not known to many. Basically, this business motivation developed from an understanding we both shared, that in the contemporary socio-economic system, personal wealth is the vehicle to creative freedom — clearly not to be confused with fulfillment of the American dream as promoted by Madison Avenue. Business success was a positive reaction to scorn from the academic science establishment for studying butterflies.

The establishment of the *Journal of Research on the Lepidoptera* was motivated by the desire for a publication capable of handling papers where full data could be set forth, plus ample space for illustrations with availability of color plates at no charge to authors. Bill had the conviction of also minimizing editing manuscripts, and controversial papers were encouraged. With emphasis on biology rather than strict taxonomy, the periodic illustration of habitats were promoted. Although possible competitiveness with the *Lepidopterist's Society Journal* concerned several workers, the *JRL* actually became a complement. A clear niche developed for both to the lasting benefit of all Lepidopterists. The Lepidoptera Research Foundation was incorporated in 1964 as a non-profit entity to publish the Journal and otherwise promote research.

Relationship with his family, wife Barbara and children Eric, Christine and Karl, was close. The Hovanitzes as a group were open, and even today with close friends and relatives represent a true extended family. No small part of immediate family involvement was with the Journal, with Barbara managing financial details, Eric's wife Karen as Assistant Editor in charge of technical matters, and the whole family stapling reprints, collating, addressing, and stuffing mailers. Family effort insured the success it has had, and will continue to be more than supportive.

Bill Hovanitz's lasting monument is in large part this Journal. We trust we are able to nurture the Journal as a facet of the most elusive testament of all — the human intellect.

TAXA PROPOSED BY WILLIAM HOVANITZ

Plebejus icarioides missionensis
Pan-Pac. Ent. 13: 187, 1937.

Oeneis chryxus stanislaus
Ent. News 48: 228, 1937.

Colias philodice vitabunda
Amer. Mus. Novit. 1240: 2, 1943
(as *C. chrysotheme vitabunda*).

Colias nastes thula
Wasmann J. Biol. 13: 2, 1955.

Journal of Research on the Lepidoptera 17 (Supplement): 7-9, 1978(79)

PREFACE TO REPRINTS

ON ECOGENOTYPICAL COLOR VARIATION IN BUTTERFLIES BY WILLIAM HOVANITZ

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Two of William Hovanitz's classic papers on ecogenotypical color variation are reprinted herein, with permission of the editors of *Ecology:* "Parallel ecogenotypical color variation in butterflies" (1941) and "Ecological color variation in a butterfly and the problem of 'protective coloration'" (1940). Not only did these papers lay the foundation for much of his own subsequent research, but in them Dr. Hovanitz synthesized ecological concepts in a way seldom seen among lepidopterists at that time. In the mid-1960s he was planning to reprint both papers, but did not, as he wanted to expand these lines of research and publish a more thorough study. However, several of the illustrations were reproduced individually in color in this journal. At the time of his sudden and untimely death 14 September 1977, he was enthusiastically preparing to resume research, long delayed by other matters, on color variation in butterflies. Thus, it seems appropriate to reprint the papers now, with this new preface. The text of the papers is unchanged except for correction of typographic errors. When possible, the photographs have been reproduced from the original color transparencies, so they vary slightly from the 1940 and 1941 figures. The 1941 maps (figure 1) were redrawn from the originals by Jamie Calhoun.

The 1941 paper presents the basic concept of parallel ecogenotypical color variation as it applies to Lepidoptera. A number of taxonomic changes have occurred since 1941 (dos Passos, 1964 and 1969). The species referred to *Melitaea* are now known as *Euphydryas chalcedona* (Doubleday), *E. editha* (Boisduval), *Thessalia leanira* (Felder & Felder), *Chlosyne palla* (Boisduval), and *C. hoffmanni* (Behr). *Argynnis monticola* Behr is now a junior synonym of *A. zerene* Boisduval, *A. montivaga* Behr is a junior synonym of *A. egleis* Behr, and *A.* (*Brenthis*) *aphirape* (Hübner) is a junior synonym of *Boloria eunomia* (Esper).

North American *Argynnis* species are often placed in the genus *Speyeria,* but in the interest of a stable and practical classification, retention in *Argynnis* seems more reasonable (Hovanitz, 1962, 1963, and unpublished). The species referred to *Coenonympha tiphon* (Rottemberg) is *C. california* (Westwood). Shapiro (1977) and Evans (1975) have reviewed the infraspecific names applicable to *Pieris napi* (Linnaeus) and *Anthocharis sara* Lucas, respectively.

The 1940 paper discusses the relationships of the subspecies *Oeneis chryxus ivallda* Mead and *O. chryxus stanislaus* Hovanitz in terms of ecological color variation. Also included is a discussion of the misuse of the "protective coloration" theory. Dos Passos (1948) raised *O. ivallda* to specific status due to the presence of anthoxanthin wing pigments (see Ford, 1941), which were absent in other subspecies of *O. chryxus* including *O. c. stanislaus.* However, the specific status of *ivallda* is a subjective matter, and some subsequent authors consider *ivallda* a subspecies of *O. chryxus* (i.e. Tilden, 1959 and Hovanitz, 1964).

Many papers relevant to ecogenotypical color variation have been published since 1941. Additional information on the species used for examples in these reprints may be found through Field *et al.* (1974) and Beattie (1971). Dr. Hovanitz's subsequent publications on ecogenotypical color variation, especially in the genera *Colias* and *Argynnis,* appear in his publication list elsewhere in this issue. Other useful bibliographies include Petersen (1947), Shapiro (1976) and Shields (1975).

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ECOLOGICAL COLOR VARIATION IN A BUTTERFLY

AND

THE PROBLEM OF "PROTECTIVE COLORATION"

WILLIAM HOVANITZ

THE DISTRIBUTION AREA OF *Oeneis chryxus* Dbld. & Hew. (Lepidoptera: Satyridae) extends from the arctic regions of North America, south through the high ranges of the Rocky Mountains, the Sierra Nevada and the Great Basin as far south as New Mexico. The butterfly is not uniformly distributed over this area but is found only in the Arctic-alpine life-zone and in the unforested ridges of the upper Hudsonian; hence, in the southern parts of its range, it is restricted to isolated "islands" on the higher peaks. The species is variable with respect to the predominant color on the upper surfaces of the wings, some individuals being a rather dark yellow-brown, others a medium yellow-brown and in extreme instances, yellow-white. The colors appear to be entirely quantitative in nature; individuals showing all different intermediate shades of color can be arranged from darkest to lightest. Within a restricted population, however, the individuals are remarkably uniform and only very occasionally are atypical examples found. Most populations consist of individuals of a rather dark yellow-brown color; occasional ones consist of extremely light or extremely dark forms.

In California and western Nevada, the species is represented by two races, a very pale, yellow-white race (*ivallda* Mead, fig. 5B) and a very dark, yellow-brown race (*stanislaus* Hov., fig. 5D). The distribution area of each of these races is shown on the map (fig. 1); the localities where the white race has been found are shown by circles and those of the brown race by triangles. The contour line shown on the map approximately encloses the habitable territory of the species, this being the Arctic-alpine and upper Hudsonian life-zones. The color shade of individuals inhabiting the various localities is shown on the

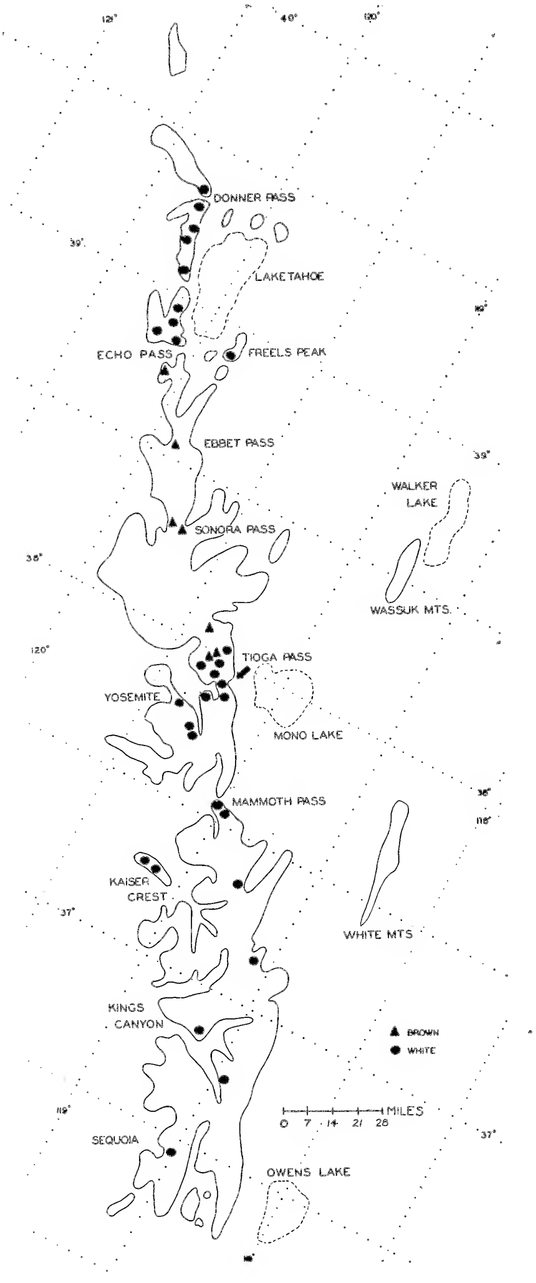

Fig. 1.—Map showing extent of Arctic-alpine and upper Hudsonian life-zones in the Sierra Nevada of California and the mountains of western Nevada. Localities where *O. chryxus ivallda* has been recorded are designated by a circle and those of *O. chryxus stanislaus* by a triangle.

diagram (fig. 2). The horizontal scale indicates the geographical position of the locality while the vertical scale indicates the shade of color, darkest at the top and lightest at the bottom; the line connecting the points gives an index of the steepness of the variation gradient (*cline* as used by Huxley, '39) between the localities. At Sonora Pass, in the center of the range of the brown race, white or light-colored individuals are taken very rarely. Between Ebett and Echo Passes the populations all lighter in color, but entirely white individuals are as yet unknown. South of Sonora Pass to a point north of Tioga Pass where the brown and white races appear to interbreed, the population of the brown race is nevertheless dark, showing no variation gradient. In the very narrow transition zone, however, the population is mixed, showing the entire range of variation from the darkest to the lightest. These facts would seem to indicate that the differences between the brown and white races are not due to a single gene, but rather to a combination of several genetic factors, and that these factors or genes are widely distributed throughout the entire range of the species though with differential concentrations. As far as one can judge without genetical experimentation, the white races from the northern and southern sections are entirely identical even though the intervening area inhabited by the dark race is at least eighty miles in extent. The shortest means of communication between the two regions is through that occupied by the brown one (fig. 1). Furthermore, as the surrounding territory is of lower elevation and is in a different life-zone, it is ecologically unsuited for the existence of this particular species; it could hardly be a region through which migration could take place. That is the status of the variation, but what is the origin of the color races and what are the reasons for their present distribution?

ORIGIN OF THE COLOR RACES

A discussion of the origin of the color races can only be speculative and theoretical, but the evidence available does allow one to comment upon several alternatives. It may be postulated: (1) That the Sierra Nevada was once entirely populated by a white race and that the brown race has either originated *de novo* in the central part or that it has come in via the high Basin Ranges from other populations of the brown form; (2) That the Sierra Nevada was once populated entirely by a brown race at

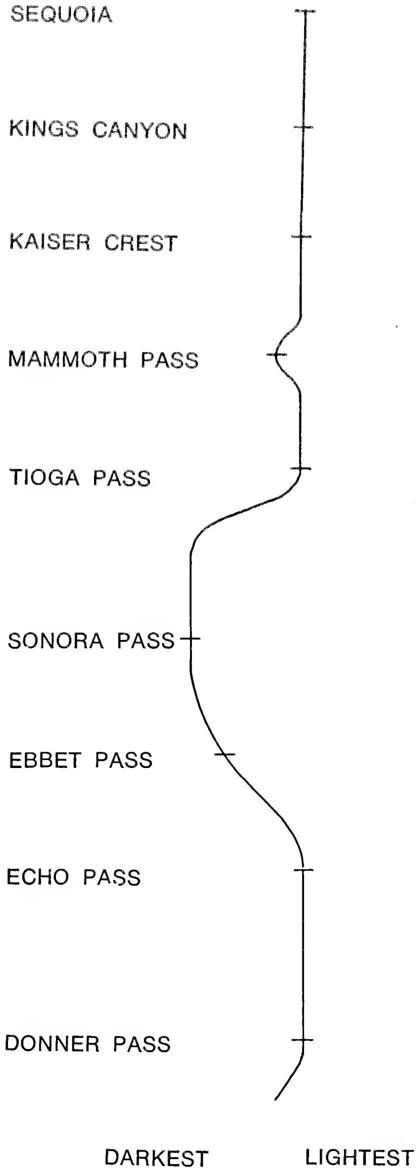

Fig. 2.—Diagram showing the shade of yellow-brown coloration typical for populations of *Oeneis chryxus* at various localities in the Sierra Nevada. The data from which this is derived were not photometrically studied (because of the lack of facilities) nor compared with a set of color standards (because the correct shade and tints were unobtainable); comparsions were made with arbitrary standards of the material itself. The diagram is, therefore, not to be taken too exactly.

either end of which genes for whiteness developed greater concentrations, or (3) That a uniform population never did exist in the Sierra Nevada. A discussion concerning these could not be conclusive when there is a total lack of paleontological evidence, but some pertinent information can be given. For example,

A. No other populations of white individuals exist in any part of the range of *Oeneis chryxus* and yet the two identical white races exist isolated from each other at the present time in the Sierra Nevada.

B. The light and dark races are interfertile and interbreed on the borders of their ranges, at which places intermediate individuals are produced. Continued interbreeding over a period of years should tend to eliminate the differences between them and produce a uniform, intermediate-colored population.

C. No other white races exist which would tend, by migratory individuals, to increase the concentration of white-producing genes in the northern and southern Sierra Nevada. Other brown races do exist which could increase the concentration of brown-producing genes. Individuals from these populations (in the Rocky Mountains) could more easily reach the Sierra Nevada via the high Basin Ranges which form a series of "steppingstones" across the uninhabitable desert areas of that region than via any other way. These are most numerous in the region directly east of the central Sierra Nevada at Sonora Pass. Other things being equal, were the influx of brown-producing genes sufficient to produce this central, brown race in the first place, it should be sufficient to change the entire Sierra Nevada populations into a single brown race.

One is forced, therefore, to ask the following questions: If the brown-producing genes have gained in concentration without the external help of migrations, what factors have allowed this increase over white-producing genes or vice versa, if the white-producing genes have gained in concentration without the external help of migrations (and it is definitely impossible to do otherwise in this case), what factors have allowed this increase over the brown-producing genes? Also, if the brown-producing genes have gained in concentration *with* the aid of migrations, what factors have prevented further spread into the regions now with greatest concentration of white-producing genes? If a uniform population never existed in the Sierra Nevada, what factors have prevented such a uniformity from becoming established and what has been the causal agent of the specific distributions observed?

REASONS FOR THE OBSERVED DISTRIBUTION

As a result of the evidence above, it can only be assumed that selection of some sort has been operative in producing the observed distributions of the white and brown races. The problem is to find the differential factors allowing for selection and then to find the specific mechanism of selection. All the possible factors which have been thought to have any bearing on selection may be placed under one of these three groups: differences in the climate, the food or the habitat. The first, climate, is not likely to be such a factor because within the Sierra Nevada, the white and the brown races inhabit the same life-zone and the white race lives both north and south of the brown race (humidity decreases southward). It may be assumed that there is no difference in general climate affecting the selection of one race in preference to the other, except wherein this may be due to some other factor indirectly. The second group, food, is likewise probably not a factor because as far as the information is available at present, the food plants of the larvae of both races are the same, namely, species of alpine grasses; more data on this subject, of course, is needed. Only in the third group, habitat, can we find a striking difference in the environment of the two races; this is in the color of the ground rock, which is the most obvious feature of the landscape above timberline (figs. 3 and 4). Soil cover at the elevations where *Oeneis chryxus* lives is scarce, and the alpine meadows where there is any considerable amount are unsuitable as a habitat. The insect lives almost exclusively on rocky terrain and the rocks, rather than plants or soil, give the predominant color to the landscape. The rock in the northern and southern Sierra Nevada, where the white race is found, is predominantly a white granite (fig. 5A). On the contrary, in the distribution area of the brown race, the central region, the mountain tops are composed of dark red rocks (fig. 5C). Jenkins ('38) and personal observations show that the country above timberline from Echo Pass to a point south of Sonora Pass is composed mostly of dark-red Tertiary volcanics and of red Miocene andesite. North of Echo Pass, as well as in a greater part of the range above timberline from north of Tioga south to Sequoia, a very light-colored Jurassic granite is decidely predominant. The accompanying photographs (figs. 3 and 4) illustrate the characteristic difference in the coloring of the

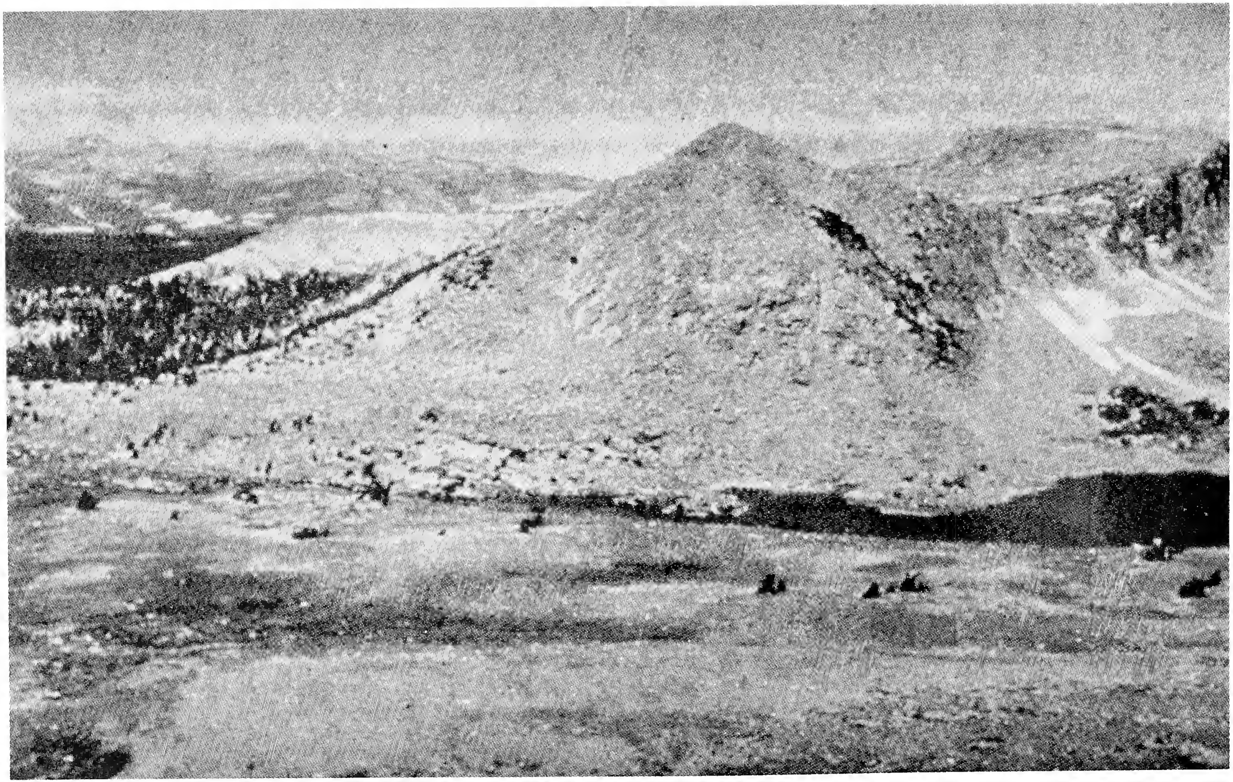

Fig. 3.—High Sierra Nevada in the Yosemite-Tioga Pass region showing the granitic aspect of the country at timberline where the white race occurs.

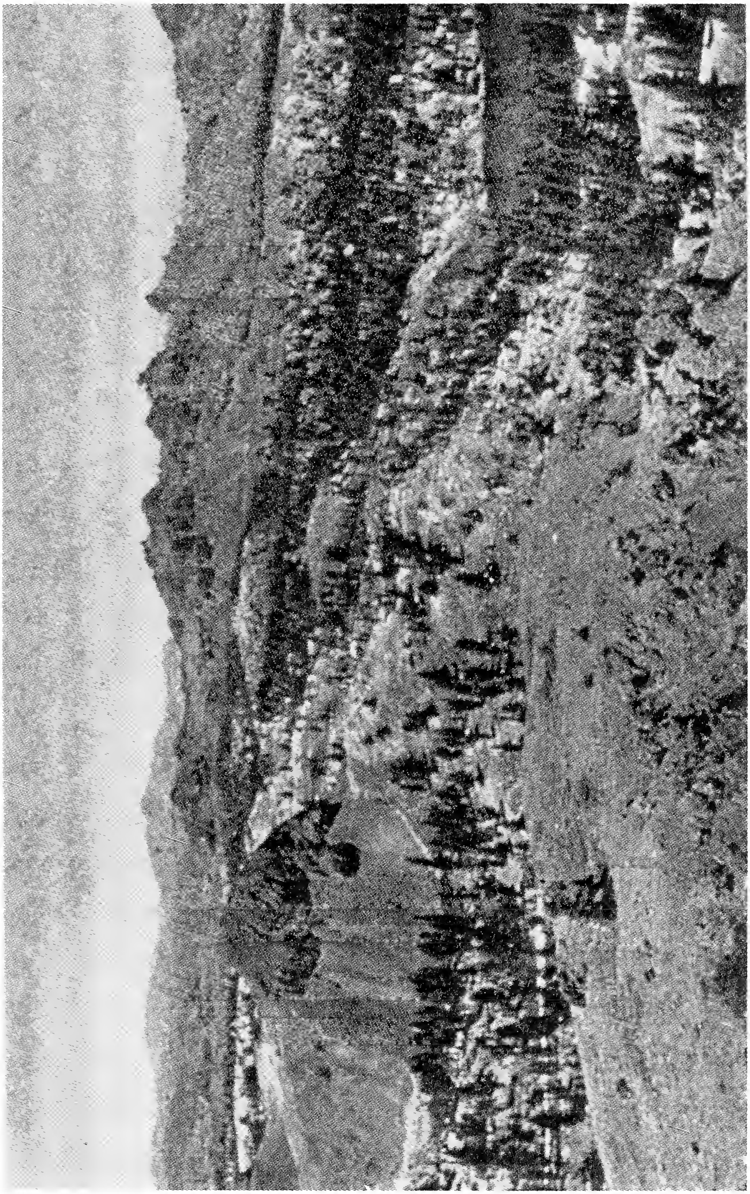

Fig. 4.—High Sierra Nevada in the Ebbet Pass region showing the dark, volcanic aspect of the country at timberline where the brown race occurs.

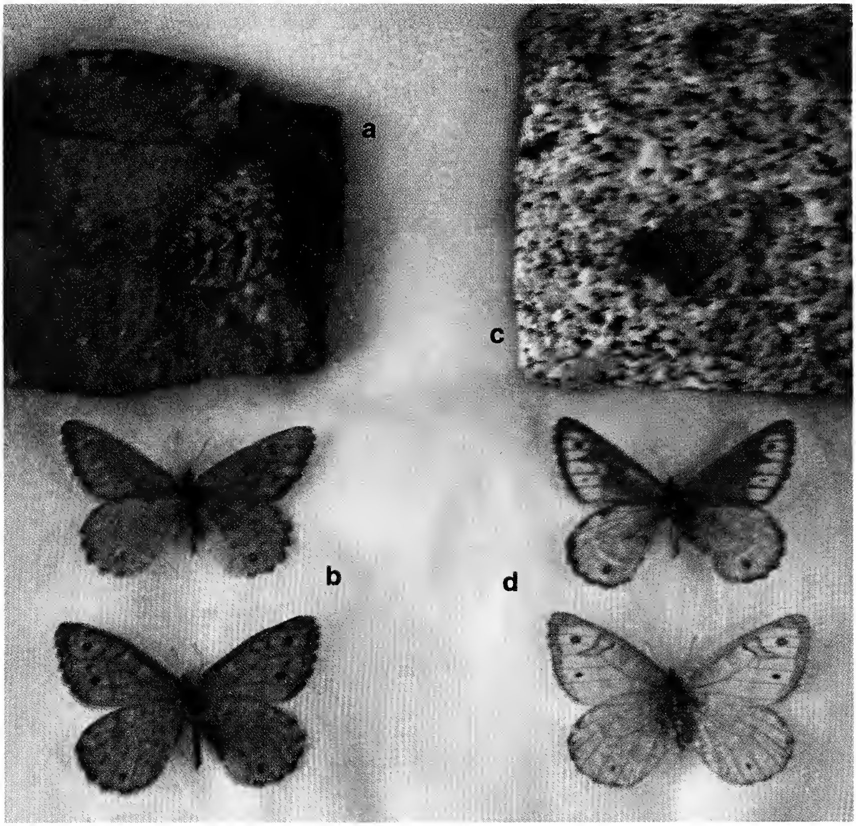

Fig. 5.—(A) An andesite rock and a specimen of the dark race with wings closed. (B) Upper surfaces of *Oeneis chryxus stanislaus* showing the predominantly darker color. Top specimen is a male and the bottom one is a female. (C) A granitic rock and a specimen of the white race with the wings closed. (D) Upper surfaces of *Oeneis chyxus ivallda* showing the predominantly white color. Top specimen is a male and the bottom one is a female.

landscape. The distribution map (fig. 1) shows that the ranges of the brown and white races almost exactly coincide with the distribution of the different kinds of rock. The presence of the more gradual gradient (fig. 2) at the northern part of the brown races' distribution can be explained by the fact that in this region there is a decreasing percentage of dark rock in relation to the light as one proceeds northward. To the south, the change is more abrupt. The "humps" seen in the diagram are also explained on the same basis; areas of dark rock are of increasing abundance in these regions.

Since the relation between the color of the butterfly and the color of the rock is the only relationship observed, the cause or mechanism of the selective effect must be found. Two possibilities are open, namely, selection by predators or selection by physiological fitness for the environment. If selection by predators is involved, one must first be able to find the predators and second, one must be able to discover that the protective color is really an aid in concealment from these predators. These requirements are seldom fulfilled in the very voluminous literature dealing with real or supposed protective coloration or mimicry. Even some most recent writers have not done this (e.g. Dice and Blossom '37; Benson '33) but appear merely to have assumed that the correlation between the coloration of some races of mammals and that of the ground on which they live is due to protection from predators. The actual proof of selection by predators (or by any other means) on any living thing in nature has not yet been shown; in fact, in most cases of supposed protection by protective resemblance, it has never been shown that the actual effective natural predator is selective on account of the supposed protection. Shull ('37) states that it is not up to the opponents of the mimicry theory to disprove the statements of the proponents, but rather the latter must present experimental evidence in favor of it first. Dobzhansky ('37; p. 164) states: "Taken as a whole, an unprejudiced observer must, I think, conclude that an experimental foundation for the theory of protective resemblance is practically non-existent." The experiments of di Cesnola ('04), Beljajeff ('27), Sumner ('35), Carrick ('36), Isely ('38), Reighard ('08) and others were conducted to prove or disprove whether cryptic or warning coloration is a factor of differential selection of prey by predators. Some of these have proven that cryptic coloration gives a selective advantage to the posessor of this coloration under the artificial conditions of predator pressure prevailing when and where the experiments were carried out, and at most can only be suggestive of wider implications. Whether or not the prey is under such predator pressure in nature and whether or not such "protective" coloration is effective or necessary under these conditions is another thing to be proven; certainly the prey must be allowed to protect itself by its own specific habits and mode of living. Heikertinger ('33-'36) and McAtee ('32) have criticized the mimicry theory rather thoroughly but neither's evidence is sufficient or convincing enough to be effective. Pearl ('30) states as the basic and minimal requisites of an observational or experimental demonstration that natural selection has altered a race in any particular instance the following: "A. Proof of somatic difference between survivors and eliminated. B. Proof of genetic differences between survivors and eliminated. C. Proof of effective time of elimination. D. Proof of somatic alteration of race. E. Proof of genetic alteration of race." No author has yet satisfied these, nor has anyone shown why one species rather than another is better adapted for existence on account of the protective colors which it possesses. Ironically enough, it would appear that the animals getting along best in nature are those which are not "protected." This should not be considered as evidence against natural selection but only as a reminder that some things can be carried too far; modern genetics assumes natural selection to be true since a method by which a genetic population change could come about any other way is unknown. In regard to *Oeneis chryxus,* it can only be stated that an unbiased student must look into all factors of the environment and this has seldom been done by any observer of "protective coloration."

A search for predators of the adult *Oeneis chryxus* has not been successful. There is no known difference (that is, no visible difference observed) between the two races in the immature stages (larvae and pupae) and they are therefore irrelevant in this connection. The adults fly only during the warmer part of the day when there is sunlight; other times they are at hiding in the relative darkness which exists between rocks, among alpine plants and such places where color is of no value. Predators, therefore, in order to be selective, must prey upon the butterflies during that very limited time of day, and chiefly when they are in flight,[1] for only at that time is the color difference shown to its greatest advantage. Other insects and birds seem to be the only predators under these conditions. Grinnell and Storer ('24) list only *Leucosticte tephrocotis dawsoni* Grin. (the Sierra Nevada Rosy Finch) and *Zonotrichia leucophrys leucophrys* (Forster) (Hudsonian white-crowned Sparrow) as whole or part time residents in the Arctic-alpine life-zone. These birds are seed eaters but occasionally capture insects. Observations have not shown them to eat *Oeneis* but these observations can only be classed as negative evidence, and not conclusive. No observations have shown other insects to eat *Oeneis* either, though further study will definitely be needed.

As stated above, there appear to be no general climatic differences between the various parts of the Arctic-alpine life-zone in the Sierra Nevada to which physiological differences between the color races of *Oeneis* might be attributed. However, microgeographic differences could exist, these being caused by different edaphic conditions, such as warmer microtemperature near the food plant due to a greater absorption of solar radiation by the dark-colored rocks. Developing larvae and pupae might be affected by the absorption of different wave-lengths of solar light (color), or by the absorption by the larvae of different chemical constituents from the food plant, which likewise might have been chemically different on account of the absorption from soil of different composition. These are factors which have received little attention from experimenters possibly because of the predatory-selection idea and cannot be verified at the present time. But as the color differences are almost certainly genetic, it cannot be assumed that the above effects change the color of the butterfly directly.[2] It may be that if a given mutated gene or, more probably, a new combination of genes (which gives the brown or white color as a bi-product) gives the insect which possesses it greater suitability for living in the habitats where the above conditions prevail, it might have a greater chance for survival.

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[1] *One of Carrick's ('36) conclusions was that movement renders as void any protective resemblance present. However, the results of this paper should not be taken too seriously; there is great doubt as to the statistical significance of the experiments made. Movement has been mentioned by many naturalists as the basic factor rendering a concealed object conspicuous; its truth is much less difficult for a critical mind to imagine than some cases of "resemblances."*

[2] *The color differences are assumed to be most probably genetic because white populations exist and develop upon dark-rock areas where these areas are smaller than the effective breeding range of an individual butterfly. White individauls from the granitic region surrounding such an isolated dark-rock area could easily swamp and make ineffective any selective effect which might be operative.*

Perhaps it may be stated that eco-genotypical variation as illustrated by the species *Oeneis chryxus* is of more common occurrence among animals than is generally acknowledged. Since most of the published data of this sort have been among the vertebrate animals, the dogma of natural selection by predation (true though it may be in many instances) has overwhelmed any theory of ecological fitness. An account of the parallel between the genetic variation and ecological preferences is being prepared which may lead to an experimental verification of the parallel between the physiological conditions of the habitat and the genetics of color in animals.

ACKNOWLEDGMENTS

The author wishes to extend his appreciation to the following gentlemen for their help in making available the facilities of their collections: E. P. Van Duzee of the California Academy of Sciences, J. A. Comstock of the Los Angeles Museum, W. B. Herms of the University of California, C. H. Harwell of the Yosemite Museum, M. L. Walton, C. N. Rudkin, Lowell Hulbirt, M. Doudoroff, R. W. L. Potts of the Cheyenne Mountain Museum, Paul Grey, C. C. Gregg of the Field Museum of Natural History, William Finley, W. D. Field of the University of Kansas, R. E. and G. E. Bohart and J. E. Cottle; also to Th. Dobzhansky for advice and criticism.

SUMMARY

The distribution of the color races of *Oeneis chryxus* in the Sierra Nevada is described. It is found that the races differ mainly in the color of the upper surfaces of the wings and that this coloration is found to be very closely correlated with the color of the habitats in which these races live. The question is raised as to the reason for this correlation and hypotheses are advanced and discussed to account for this "protective coloration," namely, selection by predators and selection by physiological fitness for the environment. The latter is thought by the author to be too severely neglected in cases of this sort and possibly to be the most probable hypothesis in this instance.

APPENDIX

LOCALITIES FROM WHICH THE MATERIAL WAS COLLECTED

Collections made in June, July or August or sporadically since 1907. (“S” means “several.”)[3]

COUNTY	LOCALITY	ELEVATION	NUMBER
Nevada	Castle Peak Ridge	8,500	about 15
“	Donner Summit	8,000	unknown
“	“Truckee”	—	—
Placer	Deer Park	7,900	1
“	Snow Mt.	—	1
“	Ward Peak	8,800	S
“	Ellis Peak	—	4
“	Ellis Peak	—	S
El Dorado	Mt. Tallac	9,000	30±
“ ”	Fallen Leaf Lake	—	S
“ ”	Pyramid Peak	10,000	—
“ ”	Echo Lake	8,000	S
—	“Lake Tahoe”	—	many
Amador	Silver Lake	8,000	3
Alpine	Freel’s Peak	—	S
“	Ebbet Pass	9,500	11
“	Sonora Pass	8,500	13
“	Sonora Pass	10,000	2
“	Sonora Pass	10,000	125+
“	Sonora Pass	10,000	28
Tuolumne	Slide Canyon	10,500	1
“	Slide Canyon	10,500	1
“	North Peak, Conness	—	10±
“	Young Lakes	—	4
“	Gaylor Lakes	11,000	15
“	Tioga Pass R. Sta.	10,000	3
“	Tioga Lake	10,000	6
“	Tioga Peaks	11,000	34
“	Mt. Dana	11,000	4
“	Mt. Gibbs	10,000	1
“	Mt. Dana	—	—
“	Mammoth Peak	10,000	S

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[3] *Most of this material was personally checked by the author; a small part of it was not and error could have come in in this part. However, all the more important localities were either collected in or the material was checked by the author.*

APPENDIX—*Continued*

COUNTY	LOCALITY	ELEVATION	NUMBER
Mariposa	Cathedral Lake	10,000?	—
“	Florence Lake	11,000?	—
“	Mt. Lyell	12,000?	—
Mono	Virginia Lakes	—	S
“	Minaret Summit	9,000	9
“	Mammoth Pass	9,000	1
“	Mammoth Crest	10,000?	2
“	“Mammoth”	—	many
“	Red Mt.	11,000?	4
“	Red Mt.	11,000?	10
“	Red Mt.	11,000?	10
“	Panorama Dome	—	4
“	Red Lake	—	2
“	Barney Lake	—	1
“	Duck Summit	—	—
“	Duck Lake	—	16
“	Skeleton Lake	—	1
“	Rock Creek	11,000	1
Fresno	Huntington Lake	—	1
“	Huntington Lake	—	—
“	Kaiser Crest	10,000	140
“	Mt. Hutching's Ridge	10,450	1
“	Bubbs Creek	10,500	1
Inyo	Bishop Creek	—	—
Tulare	Mineral King	—	1

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PARALLEL ECOGENOTYPICAL COLOR VARIATION IN BUTTERFLIES[1]

WILLIAM HOVANITZ

A Study Of The Geographical Variation within many species of butterflies in the western parts of North America has led to the discovery of many parallelisms in the color variation within these different species. Mere chance alone as the cause of this phenomenon was not considered probable as the parallelisms were found to be of great quantity and to present astounding regularities in geographical variation. After a study of the different environments in which the various species lived and of the pigment types most likely to be found under various environmental conditions, it was found possible to make a correlation between the pigment color variation and the environmental variation. It is with this correlation that the present paper is primarily concerned.

THE COLORS OF NORTH AMERICAN BUTTERFLIES

As a basis for making a correlation between pigment color variation and the environmental conditions, it is necessary to consider briefly the pigments and color patterns of the butterfly wings themselves. It will be unnecessary to go into much detail as recent reviews on the chemistry and physiology of the pigments (Wigglesworth, '39 and Lederer, '40) cover all the modern and accepted work in the field, and Goldschmidt's recent review ('38) of the experimental work on Lepidopteran patterns gives a general picture of the problems involved in their physiological and genetical determination. All that is necessary here is a brief outline of the various pigment groups in the various systematic divisions of the butterflies. Thus, each pigment group rather than each species may be handled together in correlations with the ecological factors of the environment.

The color of the butterfly wing, or of any part of it, is essentially the summation of the color of the individual scales

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[1] *The ecological part of this paper was presented at the winter meetings of the Ecological Society of America in Philadelphia, Dec. 1940. Abstract published, Hovanitz ('40c).*

on the wing; however, each scale is just beyond the resolving power of the human eye when in place on the wing membrane,[2] and the colors, therefore, appear as uniform suffusions on the wing surface. The pattern is the result of the differential distribution of the different colored scales on the wing membrane. In ordinary description, the butterfly wing is said to consist of a ground color, a pattern color and smaller amounts of other colors. The ground color, in the sense that is most often used and in the sense that I shall use it here, is any color which covers the greater part of the wing other than that occupied by the pattern elements. The pattern color is the dark color which forms the pattern bands or spots on the wing; in cases where the bands fuse or where the entire wing is overlaid with the "pattern" color, the ground color in the above sense does not exist. This pattern color belongs to the melanin group of pigments which are normally black in the butterflies but vary also to brown and gray. Few other pigments of butterflies are known as well, chemically. The yellow pigment of the Pieridae has received more attention than most others (see Lederer) and is classed as a pterine. Because the chemical classification of butterfly pigments is still in an immature stage of development, and though homologies between the pigments of various species or families would be highly useful, these unfortunately cannot be made at the present time on such a basis. Pigments will therefore be grouped into classes on the basis of (1) their visible color similarity, (2) their presence in the same species or closely related species and (3) their similarities in variation under the influence of similar environmental conditions. The following classes of partially homologous and partially analogous colors have, therefore, been arranged for use in this paper (excluding some minor colors of no interest here):

Group 1.—The black, dusty brown and gray colors which form the pattern elements, black spots and "melanic suffusion" pigment in nearly all species of butterflies. These are the melanin pigments.

Group 2.—The tawny, rufous, "red," "orange," and "yellow"

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[2] *The body of the butterfly is colored as well as the wings. This coloring is not only due to scales but also to hairs. These hairs receive in ontogeny the same pigments as the scales on the wing and, therefore, form a color pattern as well. On account of the similarity and because of the ease of working with the colors spread out on a flat surface, the wing colors alone will be discussed in this paper; it will be assumed that the body colors vary simultaneously.*

colors with a brown tint which form the ground color in the Nymphalidae, Riodinidae, Satyridae, Lycaenidae, Danaidae, and Libytheidae; also in this group is placed the yellow and white pigment found in the above families. For no other reason than for similarity of variation, these latter are placed here. They do not seem to be homologous with the yellows and whites (pterines) of the pierids and papilionids below, though the restricted orange and red spots of the latter two families are placed here.

Group 3.—The yellow, orange, and white ground color pigments of the families Pieridae and Papilionidae. The chemical classification of the pigments of this group in the Pieridae is known (they are the pterines mentioned above). The Papilionid pigments appear to be unknown chemically but are nevertheless put in this class because of similarity in color and variation with the pierid pigments.

The darkness or lightness of the wing is determined by the quality and quantity of pigments upon it and these are determined by the interaction of the various pigments. The pattern pigments of *Group One* are normally darkest of all the three groups; an increase in the area covered by this pigment would, therefore, give a darker wing. As the ground color pigments of *Groups Two* and *Three* are usually lighter in color than those of *One*, an increase in the area covered by those pigments would give a lighter colored wing. The relation of *Group One* to *Groups Two* and *Three* is therefore one of presence and absence; increase of *Group One* must be made at the expense of *Groups Two* and *Three* if the wing remains the same size. There are several ways in which the pigments of *Group One* can cover more wing area: the width of each part of the pattern may widen, the wing may be overlaid by a melanin pigment (scattered individual scales) in whole or in part, or the pattern itself may be changed by the addition of some element which was absent in the reduced condition. Goldschmidt ('38) lists the known effects of mutant genes of these types in the Lepidoptera. In considering darkness or lightness of the melanin pigments of *Group One* in this paper, no distinction will be made between these different gene and physiological reactions; the distinction between increase or decrease (or "darkness" and "lightness") of *Group One* as a whole, only, will be considered. The phylogenetic relationships involved in the various pigment changes will be left for future and more detailed papers. In the butterflies of North America, the melanin pigment itself varies but slightly in color within a species; it is invariably black and so for simplicity such variation will be disregarded in this paper.

Group Two contains a heterogeneous series of partly non-homologous pigments varying in color from white to dark rufous or tawny; for this reason, it is more difficult to analyze in terms of increase or decrease and presence or absence. Each particular pigment not only varies in area of wing covered but also its character within an area. Three main and apparently homologous types or subgroups of these *Group Two* pigments may be utilized for description: (*a*) The tawny, rufous or "red-brown" pigment which is the commonest ground color of the families listed above under this group. This pigment varies in color from a very dark rufous or tawny to a very light "faded" shade that in some groups is almost white. It is not known whether this variation is due to a chemical pigment change such as oxidation or reduction, or merely to increase or decrease in the amount of pigment deposited in the scale per unit area. In some species, a red pigment which appears to be homologous with this rufous or tawny is present (*Melitaea phaeton*); it varies from dark red to light yellow-brown and it seems most probable that a chemical change is here the factor involved. (*b*) The yellow pigments of the families above listed. This color is only of minor importance since it does not very often cover an area of more than merely spots or bands upon the wing. In a few varieties, it does assume the status of being the main ground color, however. The variation in color of this pigment is from yellow to white, due probably to a reduction in the amount of pigment deposited per unit area in the scales. (*c*) The orange and red pigments which form the border spots of the Pieridae and the Papilionidae (central spots of *Parnassius*). These are the orange and red tips of *Anthocharis*, the border spots (not the central band) of yellow or red in *Papilio* and the central yellow or red spots in *Parnassius*. They vary in a way similar to the pigments of (*a*) and (*b*) above and may prove to be chemically homologous with them. They vary not only in size but also in tint, having a continuous range of variation from yellow to red.

Group Three is much simpler to analyze than the above two. The white, yellow and orange ground-color pigments of the Pieridae and the Papilionidae are placed here. These three colors generally maintain three discrete units rather than continuous series of variation in most cases. The butterfly's wing color may be all white (leucopterine), all yellow (xanthopterine) or all orange or red (erythropterine). Only in a few populations do modifying genetic factors seem to blur the discreteness of these three. It may be that these three pigments are merely oxidation products of the pterines which are deposited in the wings at different stages of their development. Since the order of deposition of the pigments appears almost never to be anything other than white-yellow-orange rather than white-orange-yellow or some other combination, this theory seems somewhat plausible.

CORRELATION OF COLOR VARIATION AND ENVIRONMENTAL VARIATION

The method employed in determining the exact environmental factor to correlate with the pigment variation often brings up difficult problems and one cannot always attribute a given color variant to a single factor. To an ecologist this is not surprising. A living organism is in a world of interacting factors, many of which can hardly be separated from one another for analysis. In many cases, however, a single factor may be a limiting one and where this is true it is relatively simple to discover it. In order to get a rather accurate analysis, it is necessary to know as much as possible of the geographical distribution of the species studied, of its variation within as well as between populations, of the seasonal variation in species (if any), of those areas of the color pattern which are most likely to be first affected by changed environmental conditions, of the interbreeding habits of the populations studied so as to guard against error in properly separating non-interbreeding units, and a good field and meteorological knowledge of the annual climatic fluctuations throughout the range of the species, together with as much life-history data to go with this as possible. The extent to which one's correlations are correct is directly proportional to the extent to which the above factors are known. Fortunately (as will be discussed in more detail later), along the Pacific Coast certain peculiarities in the distribution of the physical factors of the environment have rendered this study invaluable aid in simplifying the correlations to be made. The following correlations were found to take place between the three pigment groups of butterflies and the environmental conditions: In the *Group*

One pigment, there is increased quantity (area and intensity on the wing) in the following regions or under the following conditions. In the *Group Two* pigments, there is an intensification or darkening of the pigments of the three subgroups and in the case of subgroup (*c*) an increase in area covered on the wing in the following regions and under the following conditions. In the *Group Three* pigments, there is often increased development of the lighter of the three pterine pigments (white, yellow and orange) in the following regions and under the following conditions.

1. In the north as compared to the south

(in the northern hemisphere)

Polar regions (northern regions in the northern hemisphere) have a reduced annual as well as seasonal quantity of solar radiation even though summer days are longer in these regions than in equatorial regions (Kimball and Hand, '36). Intensity of light is therefore less in the north than in the south. As heat upon the surface of the earth is dependent mainly upon solar radiation, cooler weather is the rule in the north and warmer weather in the south. Moisture and precipitation are usually not so dependent upon differences in solar radiation; however, available moisture may be. Water which is frozen is unavailable to plants and animals. Precipitation in the far north may be in the form of snow and remain as ice upon the earth. A given amount of precipitation in the south may, therefore, be of more importance than the same amount in the north. In considering these factors in relation to color variation later, many micro-ecological factors must be taken into account, too. A species which in the north lives on the south-facing slopes of a hill may obtain more than or as much solar radiation as the same species in the south where it may live on the north-facing slopes. Another factor which is of importance in comparing northern and southern areas is the available time interval during the year which is suitable for growth. In the north, the long, cold winters are unfavorable for life, and cold-blooded animals, at least, must hibernate. In an animal which has but one brood per year, the rate of development must be more rapid in the north than it need be in the south. Summary: In the north as compared to the south, there is in general less light, less heat, often less available moisture and less time available for growth.

2. *At lower elevations as contrasted with higher elevations at the same latitude*

Many complicating conditions arise in comparing lower elevations with higher elevations. Lower elevations have a lesser intensity of solar radiation than higher elevations (Kimball and Hand, '36). Lower elevations have a more humid atmosphere than higher elevations because of the water loss due to decreased atmospheric pressure and consequent lower temperature in the latter, even though there may be less precipitation in the former. Precipitation at increase in elevation becomes correspondingly less available because of the decrease in temperature. Higher elevations allow for a shorter available growing season for living things because of the colder seasonal and annual temperatures. The interaction of these factors do not always form a readily obvious ecological arrangement. As mentioned above, the interactions and effects must be considered on a micro-climatic basis as well as on such general terms as they are here being discussed. The time of year when these factors are critical to the organism must always be considered. Summary: At lower elevations, there is a lesser intensity of solar radiation, which is shown as a decrease in light intensity and direct heat; there is a higher air temperature and more atmospheric humidity though the annual precipitation may be lower. There is a longer available growing season per year.

3. *In areas having a dense vegetative cover as contrasted with desert or desert-like areas having little vegetative cover*

In areas having a denser vegetative cover, one must consider the indirect effects of this vegetation in causing microclimatic conditions as well as the direct ones. High solar radiation, high temperatures, high precipitation and high humidity are favorable to vegetative life. If edaphic and extreme conditions are not considered, the amount of vegetation in a given region is fairly directly proportional to the relative amounts of these factors present and available to the plants. One effect of greater vegetative cover on solar radiation is that it tends to reduce the amount reaching the surface of the earth or reflected back into the atmosphere by absorbing it in the green leaves, by absorption in the more humid atmosphere and in the clouds which pro-

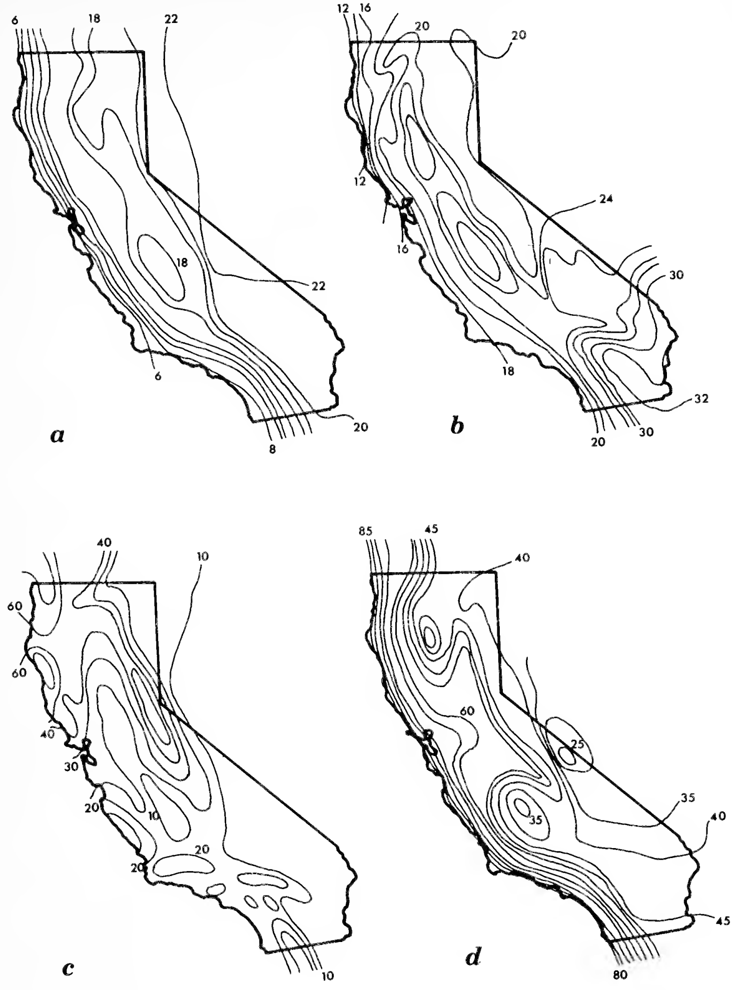
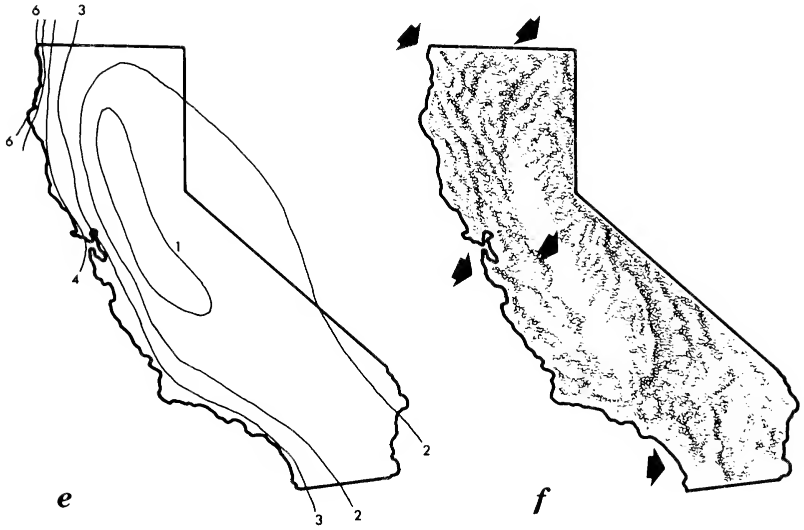


Fig. 1.—Series of maps of California illustrating the variation in climatic factors by meteorological data. (*a*) Mean annual range of temperature (°C.). Note the remarkably reduced range of temperature variation on the coast and the increased range inland. This is of importance in that the long period of favorable temperatures at the coast allows time for a lengthened development rate whereas the reduced favorable season inland makes necessary a fast development rate. Compare with map showing color races. (*b*) Average temperature in July (°C.). Note the increased temperatures inland and the decreased temperatures on the coast as well as the gradient from north to south. (*c*) Mean annual rainfall (inches). Note the increased rainfall on the coast and to the north as compared with decrease inland and to the south. Also increased rainfall on the western side of the mountain ranges and decrease on the eastern rain-shadow side. (*d*) Average relative humidity in July (%). Note the higher humidity to the north and especially along the coast and the extreme aridity of the valleys cut off from the



coast.(*e*) July daytime cloudiness (Tenths). Note the increased cloudiness in the northwest as compared with the southeast. (*f*) Showing by shaded lines the position of the most important mountain systems of California and by arrows the direction of increase of solar radiation in general throughout the state. Since solar radiation intensity is greatest in equatorial as compared with polar regions, the arrows should point directly southward. However, on account of increased cloudiness and humidity in the coastal areas (which absorb radiation) as compared with inland areas, the arrows have deviated eastward. Solar radiation intensity increases also in elevation in the mountain ranges but this could not be shown here. [Data for (*a*) to (*e*) after Brooks, Connor, and others ('37) by courtesy of the Harvard University Press.]

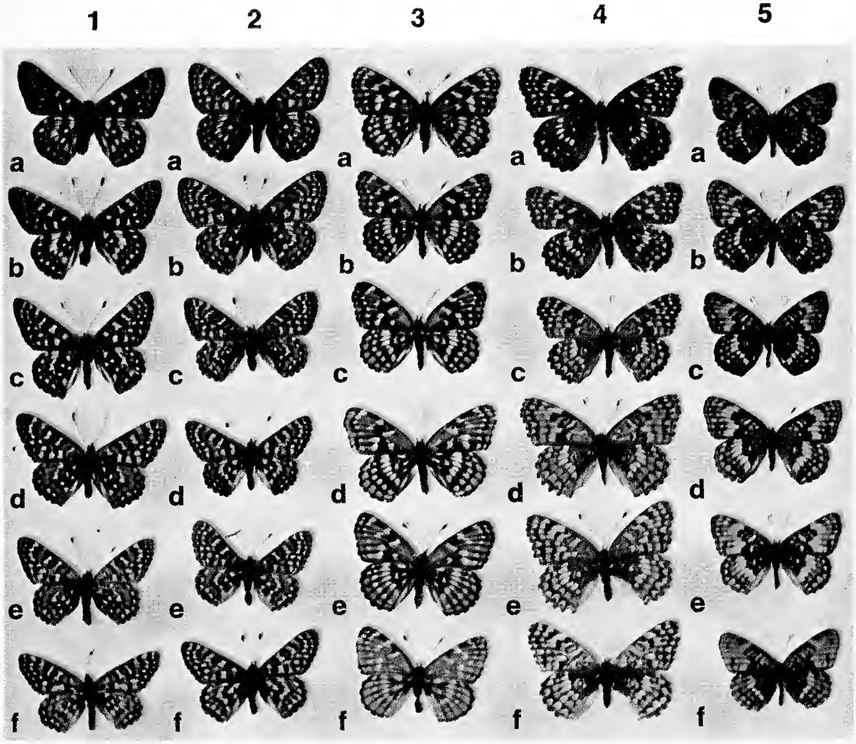


Fig. 2.—Geographical variation in five species of *Melitaea* in California and southern Oregon. (1) *M. chalcedona* (or *phaetona* section), (2) *M. editha,* (3) *M. leanira,* (4) *M. palla* and (5) *M. hoffmanni.* The order of variation from *a* to *f* is from those having the most melanin (*Group One*) pigment deposition on the wings, having the red, rufous, or tawny coloration (*Group 2-a*) the darkest and the yellow pigments (*Group 2-b*) the darkest to the butterflies having the reverse of this type of pigmentation. The darkest black shown is melanin. The grays are the rufous pigments and the whites represent the white or yellow pigment. Each specimen is used to show the type of pigmentation present at a given area on the map (Fig. 3) and should be used in conjunction with it. The specimens are intended to show only the relative amounts of the pigments present in the different geographic races and are not intended to be accurate in detail throughout the considered area concerning pattern variation details.

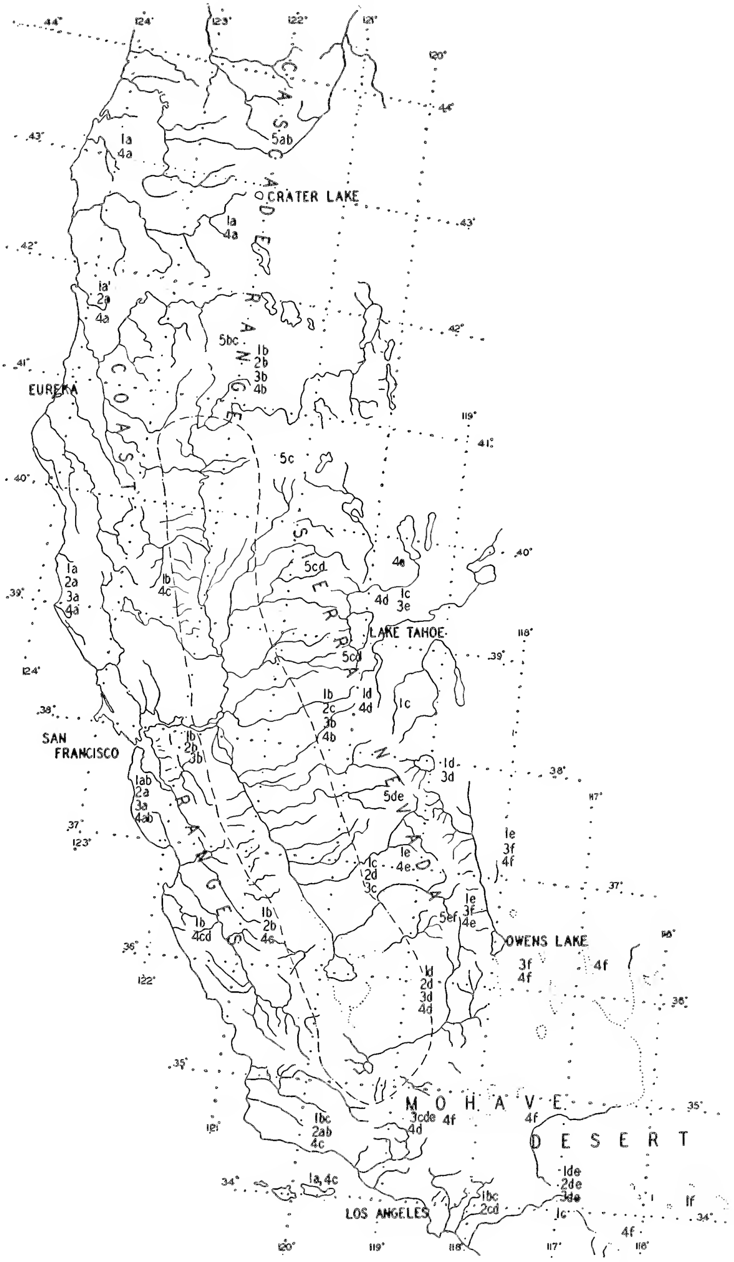


Fig. 3.—Map showing the distribution of *Melitaea* in California and southern Oregon. The numbers and letters (1*a*, 3*b*, 5*d*, etc.) represent approximate areas where populations of butterflies live having the characteristics in color of the specimen of the same designation as shown in figure 2. Comparisons should be made with that figure. The dash-dot line encloses the central valley of California where no Melitaea has been known to exist.

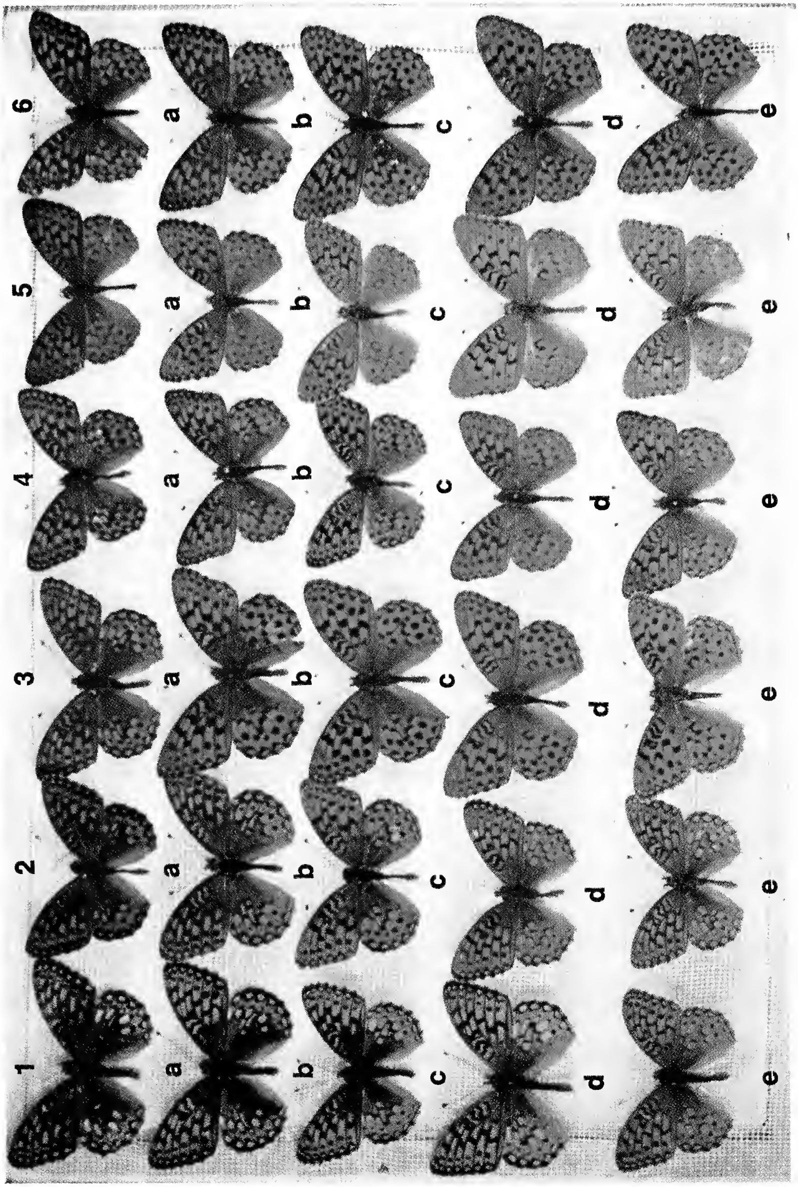


Fig. 4.—Geographical variation in five species of *Argynnis* in California. (1) *Argynnis callippe* (Coast Range cline), (2) *A. callippe* (Sierra Nevada cline), (3) *A. monticola,* (4) *A. montivaga,* (5) *A. adiaste,* (6) *A. zerene.* The ground color of the specimens figured is tawny, varying from dark at (*a*) to light at (*e*). The black pattern is melanin (*Group One*) which is most extensive at (*a*) and least extensive at (*e*). This figure should be used in conjunction with the map (fig. 5) as the numbers and letters thereon refer to the specimens shown in this figure.

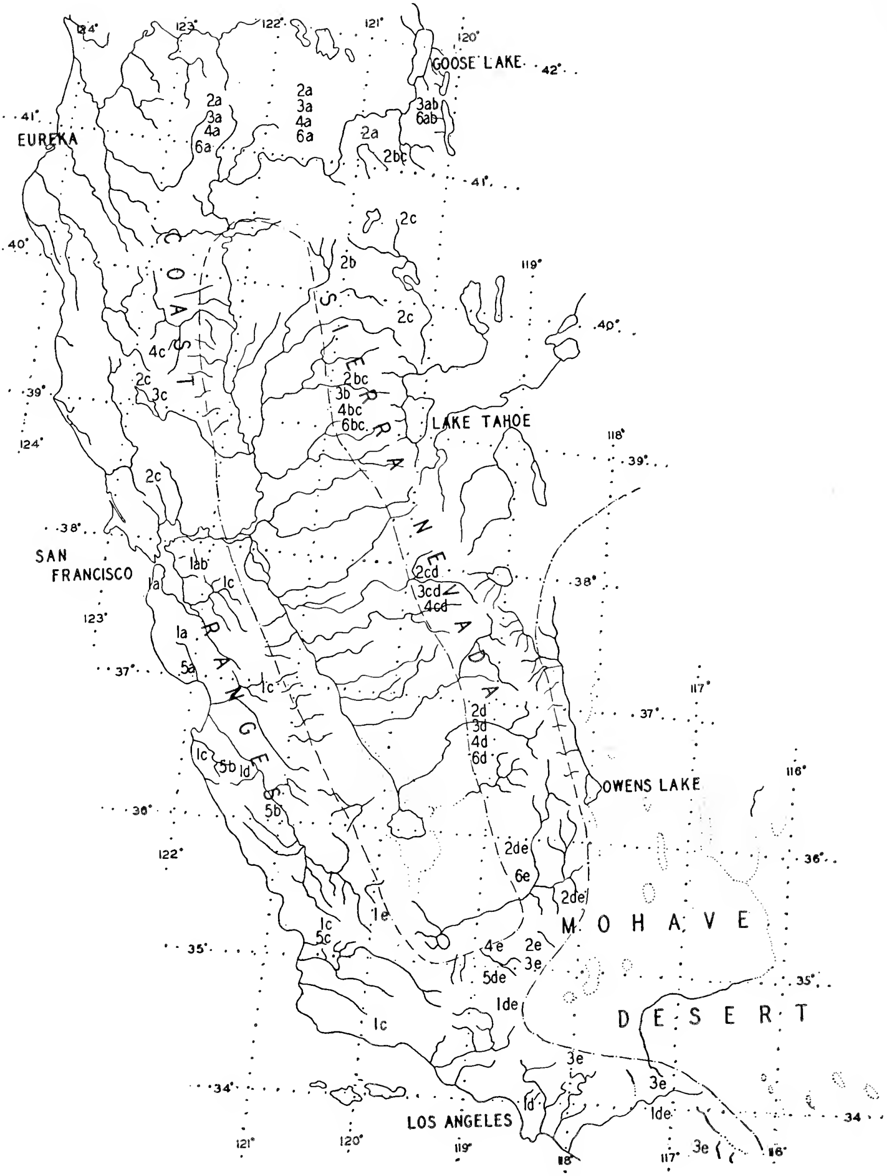


Fig. 5.—Map showing the distribution of the five species of *Argynnis* in California. The numbers and letters represent approximate areas where populations of butterflies live having the characteristics of the specimen of the same designation on figure 4. The dash-dot line encloses the central valley of California and excludes the Mohave desert area where no *Argynnis* have ever been found.

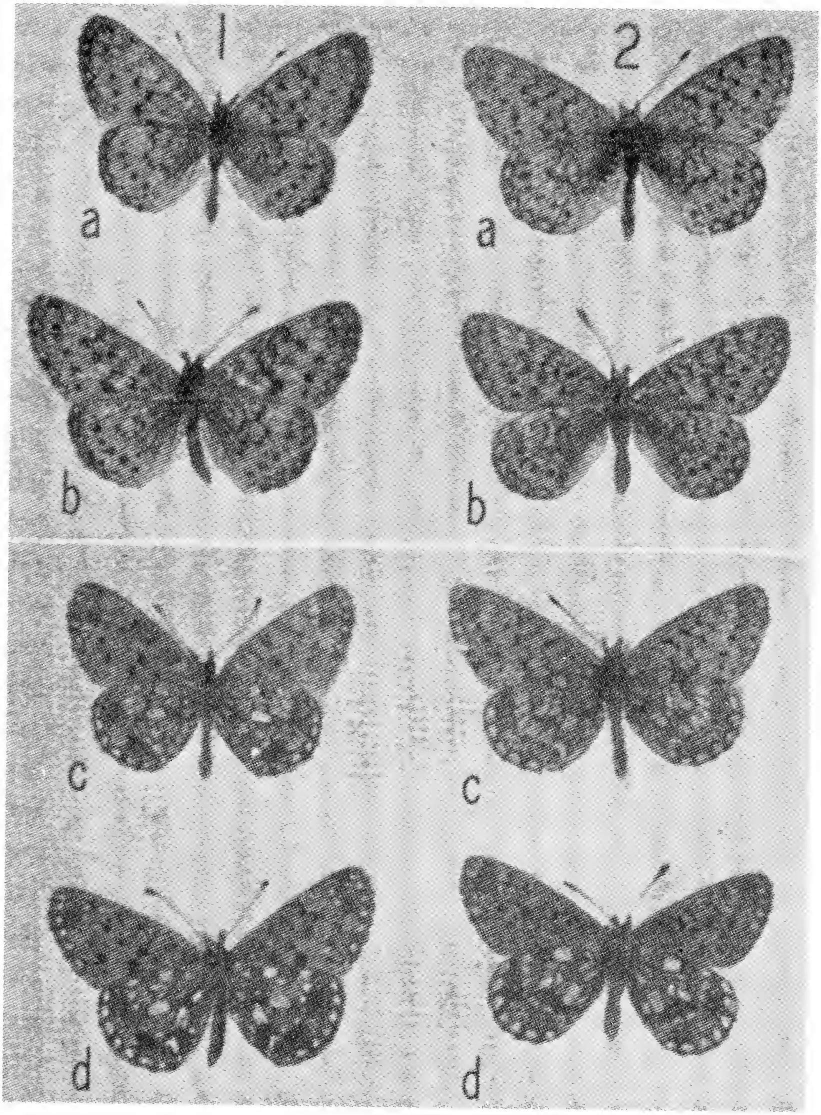


Fig. 6.—Variation in two species of *Argynnis* (*Brenthis*). 1*a*, *Argynnis selene* dorsal surface from Colorado; 1*b*, same from Newfoundland; 1*c*, same specimen as 1*a* but ventral surface; 1*d*, same specimen as 1*b* but ventral surface. 2*a*, *A. aphirape* dorsal surface from Colorado; 2*b*, same from Labrador; 2*c*, same specimen as 1*a* but ventral surface; 2*d*, same specimen as 2*b* but ventral surface.

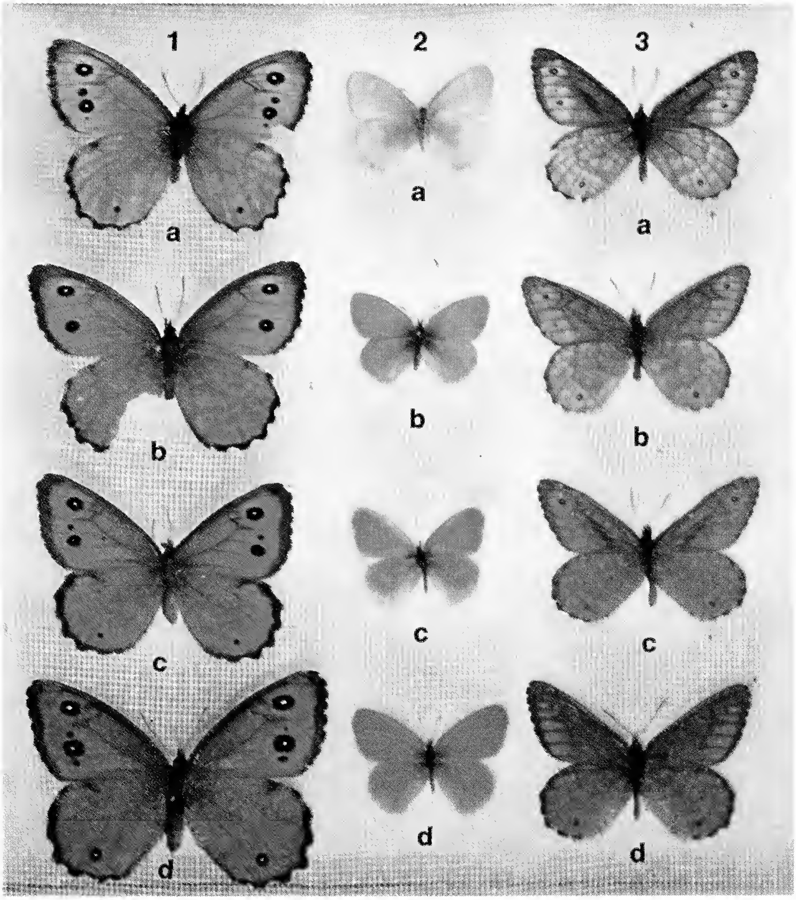


Fig. 7.—Parallel variation in the ground color of the Satyridae. 1. *Oeneis nevadensis,* 2. *Coenonympha tiphon,* 3. *Oeneis chryxus.* Specimens from (*a*) to (*d*) vary from a white ground color through yellow-brown to dark orange-brown. See text for distribution.

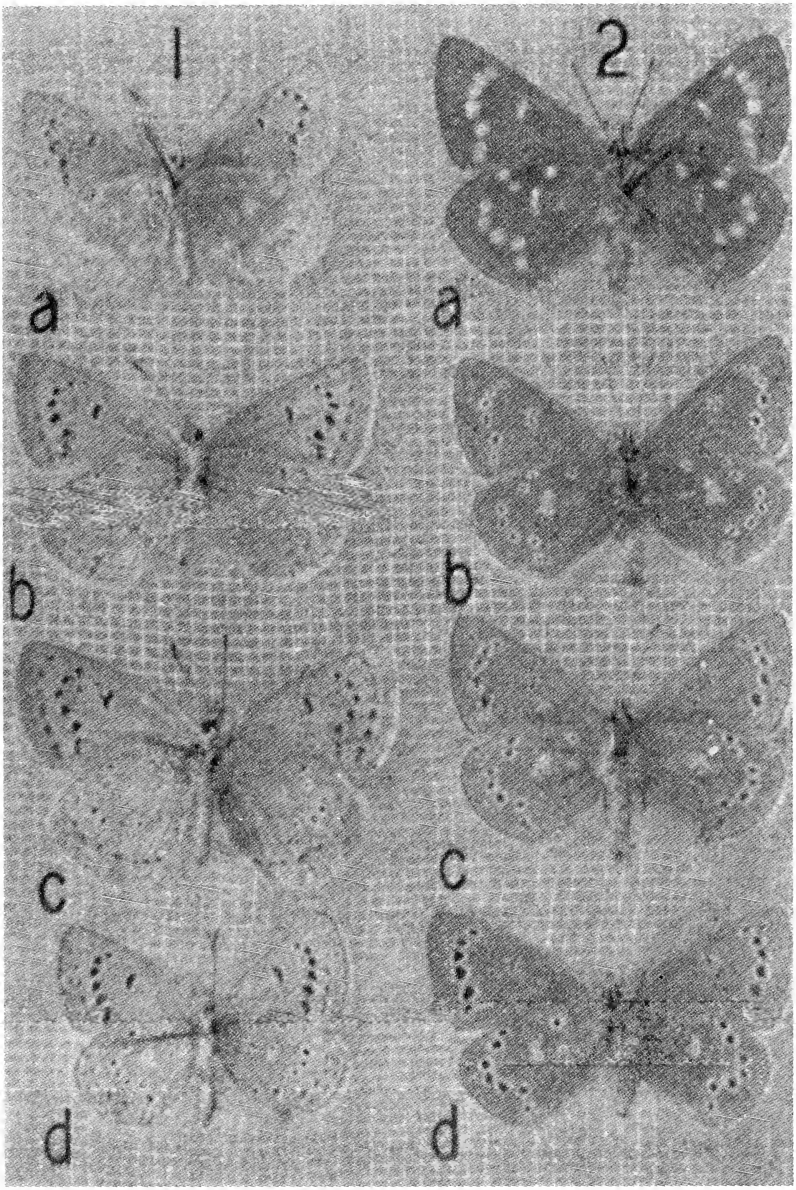


Fig. 8.—Variation in size of melanic spots in the Lycaenidae. 1. *Plebejus icarioides,* 2. *Glaucopsyche lygdamus.* See text for distribution.

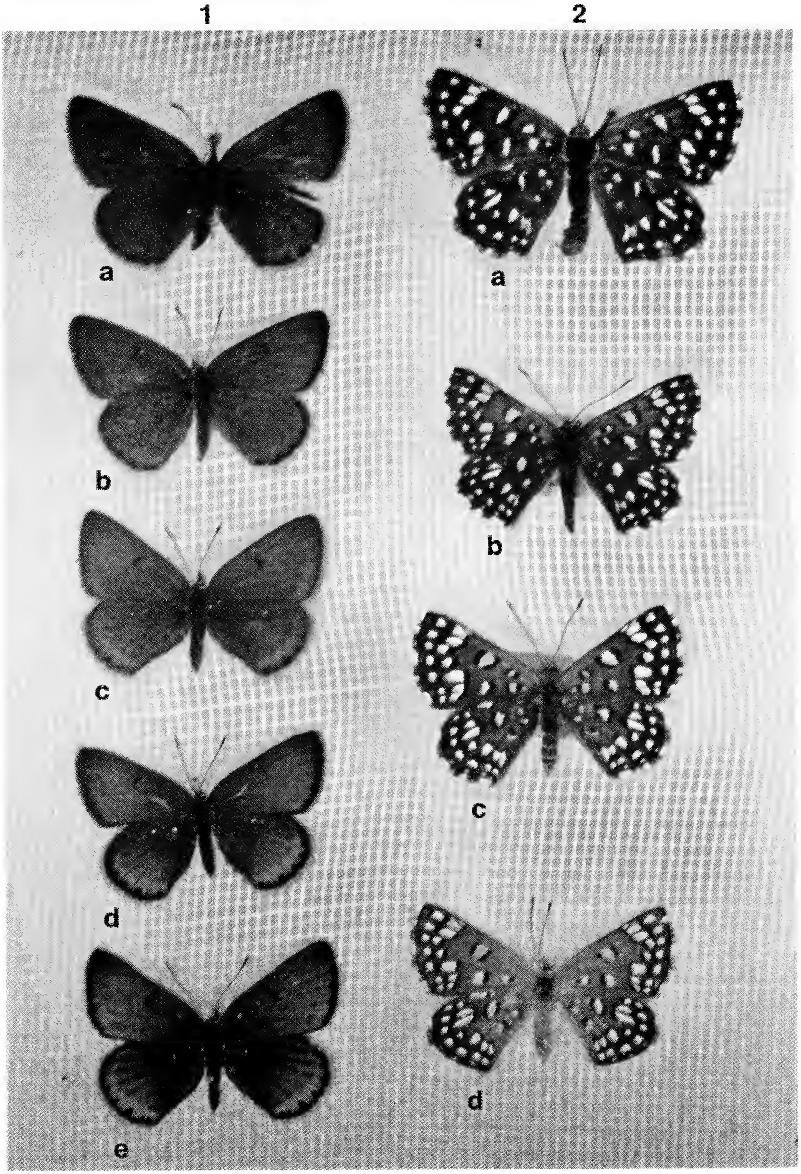


Fig. 9.—Variation in the color of the Lycaenidae and the Riodinidae. 1. *Plebejus saepiolus,* upper surface of females from California. Letters *a* through *e* refer to localities on the map (fig. 9). 2. *Apodemia mormo,* upper surface, showing increase in melanin (*Group One*) pigmentation and darkened *Group Two* pigmentation at the top and the reverse at the bottom.

duce the precipitation. Thus the relative amounts of these factors available to the insect may be greatly reduced by the vegetation itself (Popp and Brown, '36). Desert vegetation, being a gray or pale green color and with but few leaves, would also be less effective in absorbing radiation; more would, therefore, reach the surface of the earth or be reflected back, into the atmosphere. Soils in regions where there is a greater quantity of vegetative cover are usually darker in color than soils in desert areas because of the increased plant humus in the former. Such dark soils would therefore absorb more solar radiation than the light desert soils. Temperatures in areas of good vegetation are likely to be less extreme during the normal growing season of the plants because vegetation can stand little freezing temperatures; also the evaporation of water from the plants or surroundings tends to cool the immediate vicinity. On account of this more median temperature relation, the available growth period for the organism would be longer. Summary: In areas of denser vegetation, there would usually be greater humidity, greater precipitation and more cloudy days, less solar radiation (direct or reflected) and consequently less light and direct heat, and more median temperatures at least during the growing season of the year. Available development period would be longer.

4. In areas where the atmosphere is foggy, smoky or dusty as contrasted with areas where the sky is clear

In areas where the atmosphere is cloudy, foggy, dusty or smoky more solar radiation would be absorbed before it reached the earth, or would be reflected back into the atmosphere than in areas where the atmosphere is perfectly clear and clean (Kimball and Hand, '36 and Brackett, '36). Also, in areas where clouds or fog occur there is usually a denser vegetative cover and the consequent effects of this have been discussed above. Since less solar radiation is received at the surface of the earth under these conditions, the temperature will be lowered. As seen in the cool, foggy coasts and islands, and the hot deserts (Russell, '26), this is of considerable importance where the area is large enough (air mass movements play a large part in the general temperature regulations, however). Smoke and dust over the industrial regions play a large role in the amount of solar radiation reaching the earth (Brackett, '36), by decreasing the amount and also seem to have an effect in producing more fog and precipitation. Summary: Material in the atmosphere such as clouds, fog, dust and smoke will decrease the amount of light received at the surface of the earth, will tend to lower the temperature and may increase the humidity and precipitation.

5. In areas of dark colored ground cover (plants or soil) as contrasted with areas having light colored ground cover

Dark colored ground cover such as dark rock, soil or plant cover has been discussed in reference to the effects of plants above (3). Smaller or larger areas of dark rock cover some regions of the earth (see Benson, '33, and Hovanitz, '40a) and these tend to absorb more solar radiation while areas of light colored rock (such as white granite or sand dunes) will reflect a large part of the radiation striking it. In the latter case, the radiation striking an object between the sky and the earth will therefore be increased. Snow and ice may be considered as a ground cover here, too. The effects of the soil color on temperature may be slight but dark rock will absorb more heat than a light rock and on that account will be warmer. Summary: Areas of dark colored ground cover will favor an absorption of more solar radiation and an object between the sky and the earth will therefore receive less light than if the ground cover was light colored and reflected more. In the case of a dark rock cover the temperature may be raised but as given above (3), if the dark ground cover is due to vegetation, the temperature may be lowered. There is probably no effect on humidity or precipitation or upon available time for growth except in the effect of the vegetation.

6. In areas of greater precipitation as contrasted with areas of greater aridity

In areas of greater precipitation, several factors interact to produce different effects. In order to have rain, there must be clouds. Increase in clouds is followed by decreased solar radiation; this means less light and less heat. Increase in moisture is usually accompanied by increase in vegetation; the effects of this are mentioned above (3). Increase in precipitation is often followed by increase in humidity; this absorbs light and heat which might otherwise reach the earth. Summary: Greater precipitation may be accompanied by indirect decrease in solar radiation and this is reflected in less light and less heat. The direct effect of more water for the organism must also be mentioned as well as the usually greater humidity of the air in these regions.

7. *In coastal or insular areas as contrasted with inland areas*

In coastal areas, the effect of proximity to a large body of water in cases where the winds are not always from land to sea is to create a higher humidity of the air. The direct effect of this higher humidity is to absorb a portion of the solar radiation; the result, of course, is less light and less heat reaching the earth. The closer an area is to the coast, the greater is the amount of radiation absorbed. The effects of this on climatic zones can be clearly seen by reference to the map of the climates of California by Russell ('26), and life zones of California by Grinnell ('35) or the maps given in this paper (fig. 1). The increased humidity of the air is also of great importance to the existence of plant life since water loss from the leaves by transpiration would not be so great. The indirect effects of greater vegetative cover would come in here again (3). Another indirect effect of the proximity to a large body of water is the relatively smaller amplitude of seasonal variations in temperature (Brooks, Connor, and others, '37); this would allow animals a much longer available period of growth in these areas. Summary: In coastal areas, solar radiation is reduced and consequently light and heat received at the earth's surface are less. Available development time for organisms is increased because of the more even distribution of temperature during the year.

8. *In seasonally dimorphic forms: In those seasons of the year in which any of the above conditions might be seasonally restricted, or in the spring or autumn*

Seasonal variations in the environment comparable to the regional ones considered above also occur. Cooler seasons of the year in a region of high annual temperatures may be comparable to the warm season of the year in a region of low annual temperatures. The wet season of the year in a semi-arid region may be comparable to a region where the entire year is wet. In spring and autumn as compared to summer there is a diminished intensity of solar radiation (Brackett, '36); this results in less light and less heat reaching the earth. Precipitation is perhaps unaffected though available moisture may be as decreased evaporation from the soil (less solar radiation) will tend to raise the water table. Summary: Seasonal variations in the climate may be comparable to the regional ones discussed above. In spring and autumn, there is less light and less heat received at the surface of the earth, other things being equal. Precipitation and humidity are perhaps not affected.

The following table gives a recapitulation of the summaries of the eight regions or conditions above.

It is seen from this summary that if all the other conditions remain constant, light will be decreased in each of the regions or under the conditions stated; available moisture and humidity will be increased in five, neutral in two or three and may be decreased in one; temperature will be decreased in six and neutral in two; available growth period will be longer in five, shorter in one and neutral in two. It would seem that light intensity is of great importance in affecting butterfly coloration and that the other three factors may also be of equal or nearly equal importance. Under natural conditions these factors do not always vary in a parallel way but at such times, one or more may prove to be of primary importance to the organism. In some localities, different factors may affect the different species because of their different life-cycle arrangement, thus giving the effect of nonparallel variation. This may be true of such places as the Atlantic coast where increase in humidity and available moisture is southward in summer instead of northward as on the Pacific coast (Brooks, Connor, and others, '36). The result is a balance between light intensity, moisture, temperature and available period of development which at times gives a decidedly non-parallel-appearing distribution of color variation. But, along the Pacific coast, the factors seem to vary in almost perfect unison (fig. 1). Light intensity decreases to the north, precipitation and humidity increases to the north and temperature is lower to the north. With such a unity in the environmental factors, it is no wonder that the colors in even distantly related species show an extremely parallel range of variation in this region. In the extreme polar regions, *Group One* and *Two* pigments become decreased and in *Group Three,* the darker pigments become increased presumably because the short period available as a growing season is there the limiting factor.

	1. Polar areas	2. Lower elevations	3. Greater vegetative cover	4. Foreign substances or fog in atmosphere	5. Dark ground cover	6. Increase in precipitation	7. Coastal areas	8. Spring and autumn
LIGHT	decrease	decrease	decrease	decrease	decrease	decrease	decrease	decrease
AVAILABLE MOISTURE AND HUMIDITY	decrease or same[3]	increase	increase	increase	same[4]	increase	increase	same[5]
TEMPERATURE	decrease	increase or decrease[6]	decrease	decrease	increase or decrease[7]	decrease	decrease	decrease
AVAILABLE GROWTH PERIOD	shorter	longer	longer	longer	same[8]	longer	longer	same
PIGMENTS OF GROUP ONE AND TWO	darker	darker	darker	darker	darker	darker	darker	darker
PIGMENTS OF GROUP THREE	lighter	lighter	lighter	lighter	lighter	lighter	lighter	lighter

[3] *Possibly decrease because if part of water is frozen, available water is less.*

[4] *If vegetative cover is the cause of the dark ground cover, the available water and moisture would be increased through the indirect effects of the vegetation.*

[5] *Available moisture may be increased due to the lesser evaporation of water from the soil and the consequent rise in the water table. Of importance at least in the semi-arid regions of coastal California.*

[6] *At lower elevations, the amount of direct heat received from the sun is less but due to the higher atmospheric pressure and the basin phenomena of valley areas, the air temperature will be higher.*

[7] *If the dark ground color is due to the nature of the rock cover, the temperature will tend to increase. If due to vegetative cover, the temperature will decrease.*

[8] *If the dark ground color is due to vegetation, the available growth period may be increased (see 3). If due to the rock cover, it might also be increased in cold regions due to the greater heat absorption though decreased in hot, dry regions due to the excessive evaporation.*

EVIDENCE FOR THE CORRELATION BETWEEN THE COLOR VARIATION AND THE ENVIRONMENTAL VARIATION

For lack of space, it will be impossible to cover the variation of all species of butterflies; instead, a few selected examples which will illustrate all three types of color change (*Groups One, Two* and *Three*) in relation to the environment will be given here. Excellent climatic maps to accompany the distributional maps of the butterflies given herein will be found in Grinnell's Life Zone Map of California ('35), Russell's Climates of California ('26) and Brook's, Connor's and others' Climatic Maps of North America ('36). Correlation can also be made with the very generalized maps of California accompanying this paper (fig. 1).

Butterflies Having Pigments of Groups One and Two Only

Family Nymphalidae. — The illustrations (fig. 2) show a series of each of the five variable species of the genus *Melitaea* in California and southern Oregon. These species as numbered on the illustration are: (1) *chalcedona* (a representative of *phaeton*), (2) *editha,* (3) *leanira,* (4) *palla* and (5) *hoffmanni.*[9] The pigments shown are of *Groups One* and *Two,* and the parallelism in their variation is easy to observe. The darkest black color shown is melanin (*Group One*); the next lightest shade of gray represents the red, rufous and yellow-brown pigment of subgroup *a* of *Group Two*; and the lightest color is the yellow-white color of subgroup *b* of *Group Two.* It is seen that *Group One* is most extensive at the top (*a*) and least extensive at the bottom (*f*), and that *Group Two* is least extensive but darker at the top (*a*) and most extensive and lightest at the bottom (*f*). As shown on the map (fig. 3) all these species, except *hoffmanni* (5), have a very similar distributional range, and the variation in any given locality is parallel. Thus, the color variants (ecogenotypes) of all five species at the northernmost part of the map (top) are of the types *a* or *b* (the darkest) and at the southernmost part (bottom) are of the types *d, e* or *f* (the lightest). A comparison with any of the climatic maps or of meteoro-

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[9] *To save space, the extremely large number of subspecific, racial and form names applied to these species will not be discussed here. This is likewise true in relation to the other illustrations shown.*

logical data of the region will show that there is decreased solar radiation to the north, increased precipitation and cloudiness to the north, and lower temperatures to the north. There is also increased plant cover on the earth (including darker colored soil) and a higher humidity. From left to right (west to east) on the map, it is seen that the color type is darker on the west and lighter to the east. This is correlated with several factors (compare with climatic or life-zone map): the west is nearer to the ocean and hence there is greater precipitation, higher humidity, more vegetation, darker soil, more cloudiness and cooler temperatures during the growing season (air mass movements are prevailing from west to east). Specifically, several points should be noticed. At San Francisco on the coast, species 1, 2, 3, and 4 are represented by their ecotypes *a* or *b*. About twenty miles inland, still in the coast range, three of these same species are represented by their ecotypes *b* only. In southern California, the effect of the coast is most pronounced. At latitude between 34° and 35°, longitude 120° the species 1, 2, and 4 are represented on the coast by the genotypes *a, b,* or *c,* inland thirty miles by *c, d* or *e* and still farther by *f* in one or two species. (The distributional data on several of these species are much more detailed than could be represented on a map of this scale.) The effect of increase in elevation is shown in the Sierra Nevada mountains at latitude 37° or 38° where at lower elevations, the color ecotypes are respectively *b* or *c,* or *c* or *d.* At higher elevations these are *d,* or *e,* respectively. The effects of a desert habitat with little precipitation, little humidity, little vegetation and high solar radiation can be seen everywhere in the Mohave desert and the area east of the Sierra Nevada mountains. Ecotypes in this area are from *d* to *f*.

The illustrations (fig. 4) show series of five species of *Argynnis* within the state of California (one species has two isolated clines or variation gradients and is therefore shown twice). Column (1) is the Coast Range cline of *callippe,* column (2) is the Sierra Nevada cline of *callippe,* column (3) is *monticola,* column (4) is *montivaga,* column (5) is *adiaste* and column (6) is *zerene.* As shown on the map (fig. 5), the variation of all these species is from north to south. In the north there is an increase in the *Group One* pigments and a decrease and darkening of *Group Two*: the reverse takes place to the south (ecotypes *a, b* in the north and *d, e* in the south). It should be stated that since these species seem to be limited usually to a single life-zone, the elevation at which they live in the south is higher than the elevation in the north. Also the country is more arid, lighter in color and with less vegetation. *Argynnis callippe* along the coast of California is darkest at localities closest to the sea and increasingly light in color inland. The locations of the populations and the colors which they possess can be closely correlated with the landward extensions of the costal fogs. (See at San Francisco, *a* on the coast and *c* inland.) The illustrations (fig. 6) show two species of *Argynnis* (*Brenthis*) from two localities, shown here to illustrate this same sort of variation in localities away from the Pacific Coast, one father south, more inland and at a higher elevation than the other. Specimens (*a*) of both species are from Colorado, (*b*) from the northeast (Newfoundland and Labrador respectively); (*c*) and (*d*) are the same specimens as (*a*) and (*b*) but illustrate the ventral surface of the wings rather than the dorsal. An increase in *Group One* and a decrease and darkening of *Group Two* colors is present in the material from the northeast as compared to the Colorado material. It is seen that the variation takes place on both surfaces of the wings, as it also does in all the other species described.

The Family Satyridae.—Three species of the Satyridae are shown in the illustration (fig. 7). These species were selected especially to show the variation in *Group Two* pigments; *Group One* pigment varies also in many races but is not shown here, The species shown are (1) *Oeneis nevadensis,* (2) *Coenonympha tiphon* and (3) *Oeneis chryxus.* The colors of the wings are from a rufous color in the dark individuals at the bottom (*d*) to the very light (almost white) individuals at the top (*a*). Each of these species is so closely parallel to the other in color that of the three species, there appears to be no difference in the ground color when individuals of the same letter are compared (1*a* to 2*a* to 3*a,* etc.). *Oeneis nevadensis* variation is quite similar geographically to the preceding — dark in the north and light in the south. The species ranges from British Columbia to Mendocino county, California; (*d*) is from the northern locality, and (*a*) is from the most southern locality. *Coenonympha tiphon* is a species which has considerable variation throughout the western and northern parts of North America both in relation to *Group One* pigments and to *Group Two* shown here. In general, there are more races with much of *Group One* pigmentation and dark *Group Two* pigmentation in the north and the reverse in the south but this ideal situation is broken up by local influences.

The species habitat is in grasslands and it would appear that this exerts a great influence on the coloration of the butterfly. In the Northwest where the grass is mostly evergreen the butterfly is darkly colored, as it is also in the high mountain meadows of eastern California and Nevada. In the light-colored, dry-grass hills of California and southern Oregon, however, the species has the very light color shown in the figure (2*a*). There seems to be little other reason for this entire area being populated with a light form; chance seems doubtful for the same reasons as given in the former paper on *Oeneis chryxus* (Hovanitz, '40*a*). The dry grass does make a remarkably light-colored background just as does the white granite rock in the Sierra Nevada. *Oeneis chryxus* is also locally variable according to the color of its habitat, though it, too, is darker in the north than in the south in general — this darkness being due to the increase in *Group One* and in the darkening of *Group Two* pigments. The butterfly, in California at least, is light colored in areas of light-colored ground cover and dark in areas of dark-colored ground cover. A detailed discussion of the variation of this species in California has been given in Hovanitz ('40a) and will not be repeated here.

The Family Lycaenidae.—The illustration (fig. 8) shows two species of the Lycaenidae, *Plebejus icarioides* (1) and *Glaucopsyche lygdamus* (2) with a range of variation from an almost total lack of black pigmentation in the spots to a very heavy deposit. The amount of the black melanin in the spot (*Group One*) varies in the given regions and conditions in the same way as the black pattern bands in the other families. In the north there is an increase in the size of the spots; at high elevations in sand-dune areas and in desert areas the spots decrease in size. The San Francisco sand dunes are striking in the fact that at least three local races of different lycaenids (*P. icarioides*, *G. lygdamus*, and *Callophrys dumetorum*) all have developed races here with extensive white spots of a degree nowhere else attained. Figures (1a) and (2a) show white-spotted races of two of these species. Besides developing the white race in the one locality at San Francisco, *P. icarioides* has also lost its black spots in the sand dunes at Vancouver Island, at Pismo Beach (in Southern California) and along the white granitic area of the desert on the eastern side of the Sierra Nevada mountains. In addition to the variation in the deposition of *Group One* pigment in the spots on the under side of the wing, many forms show variation in the deposition of an orange pigment along the borders of the wings on the upper side. The series illustrated (fig. 9, column 1) shows the variation from the form with the greatest quantity of *Group One* pigment to the form with the greatest quantity of *Group Two* pigment. The *Group Two* pigments also become lighter in color. The species is *Plebejus saepiolus* which in California occurs in the Canadian and Hudsonian life-zone meadows of the Sierra Nevada and southern California mountains. As shown on the map (fig. 10) the variation is from an increase in *Group One* pigment in the north to an increase and lightening of the *Group Two* pigment in the south. Besides the differences in the physical characteristics of the environment due to the different geographical position, the populations in the south are at a higher elevation than those in the north and there are fewer cloudy days in the south than in the north.

The Family Riodinidae.—Only one species of this family (*Apodemia mormo*) is wide-spread in western North America. The pigments of the family seem to be homologous with those of the Nymphalidae and the Satyridae. In the far north (Washington), the representative form (*mormo*) has an increase in black pigmentation (*Group One*) and a darkening of the rufous pigment (*Group Two*) (fig. 9, column 2). In the south, these are reversed (the races *mexicanus, virgulti* and *deserti*). In California, coastal populations have an increased percentage of melanin as compared to inland ones and populations in the desert have the reverse of those in areas of greater precipitation. In the granitic area of the Sierra Nevada mountains a race with an increase and lightening of the rufous coloration (*Group Two*) and decrease in the melanin coloration (*Group One*) is present.

Butterflies Having Pigments of Groups One, Two and Three

The Family Pieridae.—Three genera of this family are of common occurrence in the western parts of North America, *Colias, Pieris* and *Anthocharis.*[10] The species of *Colias* are in such an unstable taxonomic state that it is difficult to describe the color variation and distribution and at the same time always be sure that one is remaining within the same interbreeding unit or species. *Colias* does not form local differentiated races of as small an area as many of the species above described but any given form seems to occupy a larger geographic area; this is perhaps related to the more far-flying habits of the species. Any

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[10] *On account of poor black-and-white rendition of the colors of these groups, no illustrations of pigment Group Three are shown.*

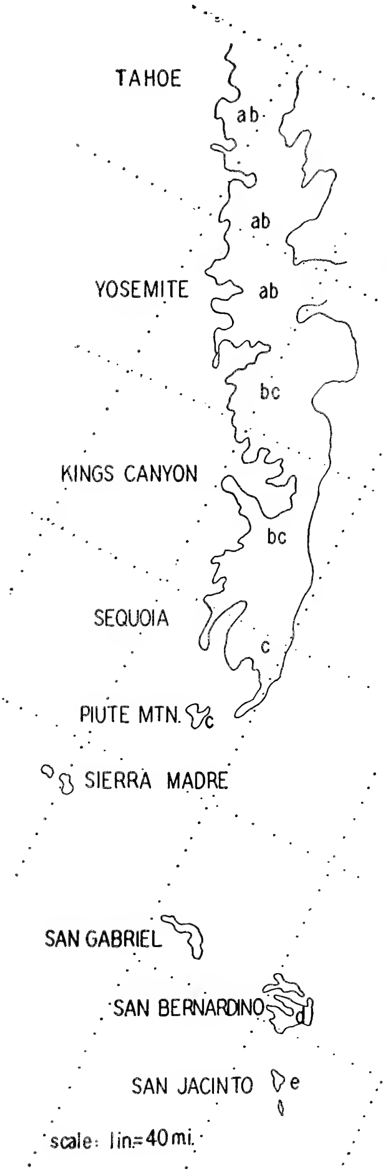

Fig. 10.—Map showing the distribution of *Plebejus saepiolus* female color variation in the California mountains. The line encloses the approximate inhabitable territory of the species from the north near Lake Tahoe in the Sierra Nevada mountains to the south in the San Jacinto mountains. The letters refer to areas where populations exist having butterflies of the same type as those designated by the same letter in figure 9, column 1. These show only representative populations, *not* all those known.

given geographical color form, therefore, must be compared to the climatic characteristics of a larger area instead of a small one. Of the three ground colors of this family (white, yellow and orange of *Group Three*), races with white color seem to be commoner in the far north and orange races in the far south. Yellow races are most abundant in the intervening territory. Areas with warm winters seem to have orange forms prevalent (the Pacific Coast and tropical areas) while the yellow and white forms are commonest in areas having cold winters (polar areas and the northeast Atlantic coast). Spring and autumn generation forms of this genus (*ariadne, autumnalis, vernalis,* etc.) have an increase in black (*Group One*) pigmentation and a decrease in orange (*Group Three*) pigmentation. Several species of *Pieris* exist in North America but the one species *Pieris napi,* will be used here to illustrate the types of variation in this group. In arid parts of the species' range, the intensity of black pigmentation upon the wings is greatly reduced (*castoria,* etc.) (fig. 11, column 3). Such forms occur in the southwestern United States at least in the summer generation. In the far north (Alaska), the forms (such as *pseudobryoniae*) have an increase in the black pigmentation as shown in the illustration (fig. 11, column 1). In the spring form in the south (*venosa*), the pigmentation is also greatly increased (fig. 11, column 2). In some of the arid mountain ranges of the Great Basin, the only yearly generation has a reduced amount of this pigment. In many summer forms and summer generations, there is present a suffusion (*flava*) on the upper surface of the wings of a yellow color (*Group Three*) which is less often found in the spring form. *Anthocharis* illustrates better than *Pieris* and *Colias* the variation in this family. It has present all three groups of pigments whereas the latter have only two. The orange or red apex spots of this genus represent *Group Two*-subgroup *c* pigments. In Alaska, a form with a very dark-red apex spot, an increased amount of black pigment and a white ground color occurs. In the south (California), the summer forms have a smaller and lighter apex spot, less black pigmentation and an increase in a yellow ground color suffusion in the area of the white (*sara*). In arid Utah, the only yearly generation of this species (*browningi*) has a small, light-red apex spot and a reduction of black pigment of a degree no where else attained. The spring generation of the species in coastal California (*reakirti*) has a greater amount of black pigmentation and few-

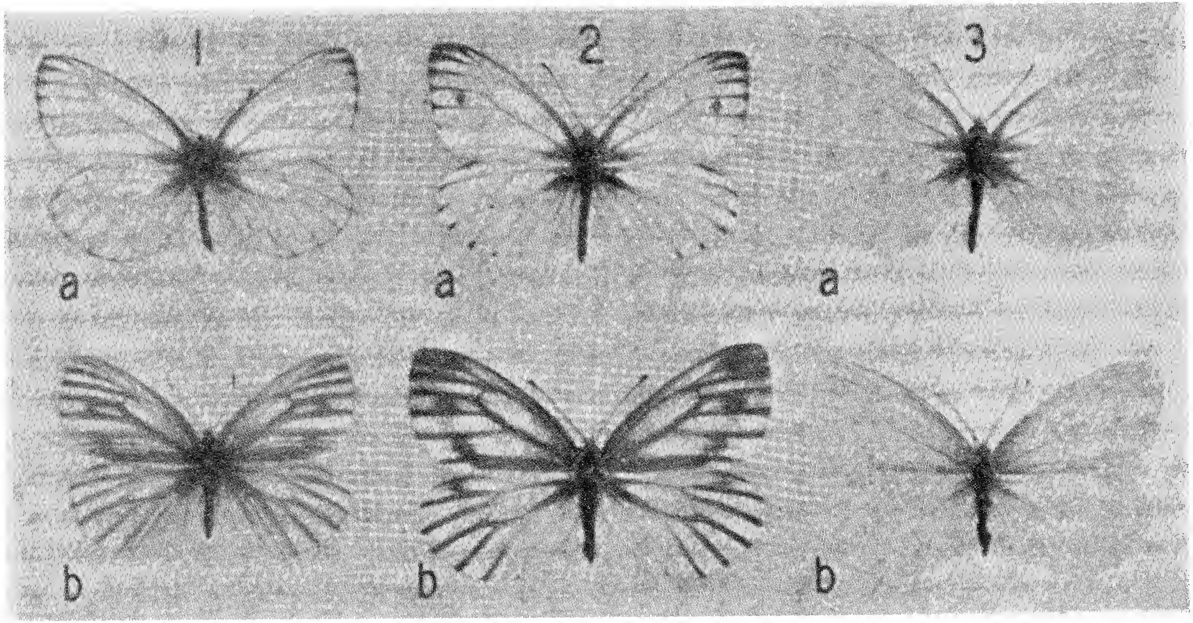

Fig. 11.—Variation in *Pieris napi*. 1. Alaskan form, (*a*) male, (*b*) female. 2. Spring generation form from central California, (*a*) male, (*b*) *female*. 3. Summer generation form from central California, (*a*) male, (*b*) female.

er yellow pigmented individuals than the summer generation in the same place. A form in the high Sierra Nevada mountains (*stella*) which exists in the white granitic areas is always yellow in color. In the closely related species, *cethura*, the ground color is yellow in Arizona (*pima*) and white in California (*cethura*). In the Mohave desert of California, a form (*deserti*) occurs in which there is a complete loss of the orange tip (*Group Two*) from the apex of the wings and a reduction in the amount of black (*Group One*).

The Family Papilionidae.—In the two genera of this family, there are present all three pigment groups. In *Papilio*, there are few examples of the ecological variation because the species are rather far-flying and not very variable locally. *Papilio eurymedon* shows some variation. In a British Columbia form, the pattern pigment (*Group One*) covers more area than the form in the lowlands in California, though a forest form of the California mountains (*albanus*) has again an increase in the *Group One* pigment. This dark California form does exist at a higher elevation than the lighter form but this seems to be correlated to the forest habitat of the dark one. *Papilio rutulus* varies little in *Group Two* pigments but does develop a form in the southwestern semi-arid regions in which the yellow ground color (*Group Three*) becomes more orange in tint. In the north it is pale yellow. The eastern *turnus* seems to produce such an orange form in the southern parts of its range. In the north, these forms develop an increase in the black pattern elements (*Group One*) and a lighter yellow-ground color (*canadensis*) (*Group Three*). In the genus *Parnassius*, both widely distributed North American species (*clodius* and *smintheus*) develop races with an increase in melanin pigmentation (*Group One*) and a darkening of the red spots (*Group Two* subgroup *c*) in the far north (*claudianus*, etc.). In the southern and arid parts of the ranges of these species, the *Group One* pigments are decreased and the *Group Two* pigments are a paler red or orange color (*altaurus*, etc.).

DISCUSSION

Parallel variation in the morphology, color and physiology of non-interbreeding organisms has been observed in several major groups of animals and plants. There appears to be, however, no one source where all the evidence in these divergent fields has been summarized or reviewed. Reinig ('37) gives the best recent summary of the work dealing mainly with the color variation in European Lepidoptera. He appears to consider the genetic, the physiological and the ecological evidence but does not make any conclusions as to a correlation between the color types and any specific environmental factors. However, he includes a rather extensive bibliography on the earlier work in the field; this will not be repeated here. Recent treatises on evolution by Goldschmidt ('40) and Dobzhansky ('37) as well as the volume on ecological animal geography by Hesse, Allee and Schmidt ('37) also touch on this field in their reviews of the literature. Parallel variation in plants has been extensively covered by Turesson ('22 and '30) and Clausen, Keck and Hiesey ('40) in relation to the influence of the environment. Vavilov ('22) has formulated the "law of homologous series in variation" on the basis of parallel variation in plants though he does not bring adaptation into his discussion. Work in closely related fields (not in butterflies) may be mentioned by referring to the work of Dice ('40a) and Sumner ('32) on rodent ecotypical coloration (*Peromyscus*), Alpatov ('29) on the geographical races of the honey bee (*Apis*), Tower ('06, '18) on the color variations in the potato beetle (*Leptinotarsa*), Allen ('74), Beebe ('07) and Rensch ('29, '36) on the variation and distribution of birds in relation to color, Enteman ('14) on coloration in wasps (*Polistes*) and Dobzhansky ('33) on parallel color variation in ladybird beetles (Cocinellidae). Much of the work done on mimicry in butterflies should probably also be mentioned here as perhaps being in many cases only parallel ecological variation causing convergence of color pattern appearance (Punnett, '15; Poulton, '08, '09, '31; Wallace, '71; Heikertinger, '33-'36; Eltringham, '10). The regional or local area mimicry would also belong in this class.

Vavilov (as mentioned above) described the remarkable regularities in variation existing between various species of plants and thereby formulated his "law of homologous series in variation." He thus showed that homologous and analogous variations in different species are of common occurrence. The intensive and extensive work of the *Drosophila* school of geneticists has provided excellent material for the study of homologous gene mutants in different species (Sturtevant, '40), an amount of work which could hardly have been accomplished with any other animal. Definite genetic evidence is now accumulating to prove the commonly accepted idea that closely related species may be very similar in genetic constitution and that genes having similar action upon the phenotype of the animal may be homologous in the different species. The importance of this fact to parallel variation is that these mutants should tend not only to produce varieties within the different species having similar phenotypes, but also, if these homologous mutants gave a survival advantage to the phenotype of the possessor under a similar set of environmental conditions there should come about as the result of natural selection parallel and homologous series of variation. It should be realized, however, that *different* genes can give *identical* physiological effects. Besides genetic homologies, direct physiological homologous effects upon the phenotype of an organism can be produced by the direct action of similar environmental conditions (Goldschmidt,'38, Harrison, '32, Harrison and Garrett, '26, Allee and Lutherman, '40, Gerould, '16, Standfuss, '98, etc.). In most cases where one is dealing with wild populations, the effects of the environment and the effects of the genom may be difficult to differentiate without laboratory analysis, and these two effects may also be additive in their phenotypic expression. (See Turesson ('22).) This is especially the case where a single species varies seasonally as well as geographically. In the discussion of parallel variation above no attempt has been made to give a clear separation between hereditary, parallel, color variation and the environmentally modified variation though in many cases experimental evidence is available to suggest such a differentiation. A great deal of work has been done by various experimenters on the direct physiological effects on color of temperature, humidity, and to a lesser extent, light. It is generally agreed that lower temperature, higher humidity and a lower intensity of light[11] are conducive to the production of a greater quantity and a darker quality of the pigments on butterflies which fall in the first two groups given in the preceding sections (for reviews, see Chapman, '31 and Reinig, '37). These physiological results are therefore in complete agreement with the zoogeographical and ecological results developed in this paper.

The non-acceptance of the theory of the inheritance of acquired characters makes it a more difficult problem to explain the genetic, parallel color variation of this type on the same basis. It becomes necessary to prove that a particular color variety is better adapted or fitted to a given environment and therefore has a better survival value or reproductive advantage over other types under the same

[11] *The complete absence of light is, in many cases, accompanied by a reduction in pigment formation and deposition.*

conditions. This proof has never been obtained under natural conditions. It has, however, been suggested many times and must be considered as being an unproven but highly probable hypothesis. Kühn and von Engelhardt ('37) have shown that a genetic mutant of a moth which has as a phenotypic character the suffusion of the wings with melanin pigment (*Group One*) has an increased viability under conditions of lower temperature and increased humidity than the same moth without the single mutant effects. It has also a slower genetic development rate which would seem to fit in with the longer development time usually possible under these environmental conditions. This study is perhaps the nearest approach to proving how a genetic melanic mutant might be better adapted to living under the accompanying environmental conditions that has ever been made.

It seems that none of the theories of genetic melanism (increase in *Group One* pigment) in animals in the industrial centers of the world (see Hasebroek, '34 for review) have as yet been found to be entirely successful. The suggestion may be made here that perhaps the cause of the increase in melanic forms in these regions is not to be found in the direct effects of the industrial material with which the air and vegetation of the areas are contaminated (such as smoke, soot, chemical vapors and deposits, etc.) but rather may be looked for in the indirect effects of these in reducing the light and direct heat penetration of the atmosphere and in the greater absorption of that which does penetrate it. The effects of continued dust in the air are very likely to be similar to those produced by fog and clouds; city air contamination is high and the effect on light penetration is great (see Brackett, '37). Considering the matter in this way brings the problem of industrial melanism closer to the essentially similar natural "melanism" described above; these two problems may have the same basic foundation in ecology and population genetics. What remains to be proved in any case is the physiological fitness of one type over another under these essentially similar environmental conditions. Ford's theory ('37, '40) of industrial melanism appears no closer to proof than any of the others. He suggests that mere selection of dark forms over the light could not explain the melanism but instead that the dark forms (when the melanic gene is dominant) are naturally hardier than the light forms throughout the range of the species. They are selected against because they lack cryptic coloration, except in industrial areas where the advantages of hardiness overrules the advantages of cryptic coloration. The author does not see how this clears up the problem since it still leaves an unknown advantage to be conferred on the melanic forms in industrial areas. The variation of butterfly pigments in relation to the physical environmental factors seems, according to all experimental evidence, to be too great to have much effect on cryptic coloration. The variation of *Group Three* pigments is irreconcilably opposed in "protectiveness" to the pigments of the other groups. In light-colored habitats, *Groups One* and *Two* become lighter in color but *Group Three* becomes darker. Certainly this is no adaptation in the sense of cryptic coloration, though there seems to be no doubt that there is adaptiveness involved somewhere in the developmental physiology of the butterfly. No doubt, too, in the case of some species and especially in the case of larvae that feed in the daytime, protective coloration does lead to a differential selection of colored types. This is, however, not the place for an extended discussion of the merits of "protective coloration" (see Cott, '40, for review); it is intended only to suggest that good theory firmly established as dogma should not be put up as a wall to block efforts to find new scientific facts.

Dice ('40b) correlates the pelage color of a deer mouse (*Peromyscus maniculatus*) across North Dakota with the environmental variation across the same terrain. He finds a gradation in pelage color from light-colored in the west to dark-colored in the east and correlates this with a lighter soil cover in the west than in the east. Also, there is present an increase in elevation, a decrease in precipitation and a more arid character of the vegetation in the west as compared to the east. These results may be compared with those presented in this paper. The data of Benson ('33), Dice and Blossom ('37) and Hovanitz ('40a) in which animals possess a body color (or wing color) closely similar to the substrata on which they live can also be related in the same way, though in these cases soil color seems to be the only variable. Dice ('40) presents evidence derived from variation in small animals that pelage color is almost always variable in direct relation to the color variation of the soil habitat. He shows that similar color races may be developed at isolated points if the environmental conditions are parallel at those places; he also concludes that the subspecies is primarily an ecologic unit. Essentially these same conclusions have been arrived at and put into modern eco-genetic terms as early as 1922 by Turesson (already mentioned). The present author believes that they are true also for butterfly variation, though he would include not only the subspecies but the species as well, thus bringing in Darwin's "Origin of Species by Natural Selection."

The only rule of color variation definitely formulated in the literature is known as Gloger's (cf. Rensch, '36). This states that in warm-blooded animals, races living in warm and moist regions have more melanin pigmentation than races living in cooler and drier regions and that races inhabiting arid, desert regions have more yellow or reddish pigmentation. The rule was found to hold in a significant number of cases although there were exceptions. In insects, various authors (Dobzhansky, '33; Reinig, '37; Hesse, Allee and Schmidt, '37; Enteman, '04) produce or review evidence leading to rather diverse opinions on color variation, but in general seeming to agree that darker pigmentation increases under humid and cool conditions, and that the lighter pigments increase under dry and hot conditions. This is not exactly the order in which the pigmentation variation takes place in warm-blooded animals but it is suggestive of the same trend. Obviously, the physical conditions (temperature and humidity) do not vary together but rather do so mostly at random (though not always), the result being visible in the diverse climates of the hot, humid tropics, the hot, dry tropical deserts, the cold, humid arctics and the cold, dry arctics. Many apparent exceptions and reversals of the rule are therefore to be found depending on the particular group being studied. Many authors (cf. Dobzhansky, '33 and Enteman, '04) have used such terms as "centers of light forms" and "centers of dark forms" to describe the parallel color variation found since this does not make necessary an interpretation of the physical and biological factors involved in the variation. These centers of pigmentation are shown to be centers of certain physical conditions such as aridity, high temperature, etc., though they might, more specifically, have been said to be centers of low precipitation, low humidity, high temperature, high solar radiation, fast animal development and light colored soil.

CONCLUSION

It may be concluded that butterfly color variation is closely correlated with the variation in the environmental conditions. Because most subspecific color variations found in the wild are genetic, the type of variation may properly be termed ecogenotypic (after the terminology of Turesson). As many of the color variations are not protective or "adaptive" in themselves, it is believed that the colors are only a secondary product of some physiological change in development, metabolism or "hardiness" which are of primary adaptive value. It is believed that proof of any theory of adaptive coloration must be accompanied by proof of the mechanism of the selection and this proof has not yet been presented for any phase of the problem.

Four environmental conditions are found to be of significant interest in the correlations with pigment color variation: increase or decrease in temperature, increase or decrease in precipitation or humidity, increase or decrease in solar radiation and rate of development of the organism.

SUMMARY

1. The pigment colors of North American butterflies are divided into three basic groups for comparing their variation with the variation of the environmental conditions. These are: *Group One*: the black, brown and gray melanin pattern elements found in all families, *Group Two*: the tawny, rufous, red, orange and yellow colors with a brown tint which form the ground colors in the Nymphalidae, Riodinidae, Satyridae, Lycaenidae, Danaidae, and the Libytheidae; also the yellow and white colors of these six families and orange and red spots of the Pieridae and the Papilionidae, and *Group Three*: the white, yellow and orange ground color pigments (pterines) of the Pieridae and the Papilionidae.

2. The variation of each of these three pigment groups is correlated with certain geographic regions and conditions in which the insects live. It was found possible to correlate lower temperature, increased humidity, increased precipitation, decreased solar radiation, and decreased development rate in most cases with the following pigment changes: *Group One* pigments increase in area and intensity on the wing, *Group Two* pigments increase in intensity or darkness and may decrease or increase in area and *Group Three* pigments show increased development of the lighter of the three pterine pigments (white, yellow and orange).

4. The conclusion is reached that these factors play an important part in the color variation of butterflies and that, therefore, the color variation may be considered adaptive.

5. It is also concluded that contrary to established dogma, the adaptiveness of animal coloration need not only be "protective" but may be only a secondary product of a more fundamental function in the physiology of the animal.

6. Correlations of butterfly color variation with evidence from other animals is given to show the parallelism in the variation and in the ecological characteristics of the environments.

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Journal of Research on the Lepidoptera 17 (Supplement): 66-76, 1978(79)

PUBLICATIONS OF WILLIAM HOVANITZ

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1936

1. Notes on some California butterflies. *Pan-Pacific Entomologist,* 11(4):190-192. ["1935"]

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131. Distribution and geographical variation of *Argynnis adiaste* (Lepidoptera: Nymphalidae). *Journal of Research on the Lepidoptera,* 18: in press. [left by WH as unfinished manuscript, finished by Scott E. Miller]

Cover illustration: William Hovanitz, on the Canol Road, Yukon Territory, Canada in July, 1973. Photograph by Karl Hovanitz.

THE JOURNAL OF RESEARCH ON THE LEPIDOPTERA

Volume 17 *Supplement* *1978(79)*

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KENTUCKY LEPIDOPTERIST: A publication of the Society of Kentucky Lepidopterists appearing as a quarterly. Write Dr. Charles Covell, Dept. of Biology, University of Louisville, Louisville, Kentucky 40208, for membership data.

REGIONAL SOCIETIES: It occurs to us that a listing of regional societies would be useful for several reasons. Please supply us with relevant information and we shall assemble such a listing.

BOOKS FOR SALE: Romanoff, N. M. Memoires sur les Lepidopteres. Vol. 1-7 and 9. With 61 plain and 69 colored plates and 3 maps. Recent H. calf. This excellently illustrated work is the rarest in modern literature on Lepidoptera. It includes contributions on Asian butterflies by Romanoff, Grum-Grzhimailo, Staudinger, Cristoph, Snellen, Heylarts and others. Robert Fagen, R. D. 1 Box 24, Glen Mills, PA 29342.

FOR SALE: Butterfly and moth collection, mainly southern Michigan and Tennessee; 4,200 specimens, all mounted with complete data, Cornell drawers and unit trays, nearly all specimens perfect, pupal skins and parasites; 1,300 Catocala, 1,100 Hesperidae, includes good series of E. mitchellii, C. muticum, H. ottoe, and O. powesheik from Michigan. Will consider best offer. Complete inventory upon request. Wayne Miller, 1476 North Hills Drive, Kalamazoo, Michigan 49007.

SUPPORT THE XERCES SOCIETY, a non-profit organization dedicated to the protection of habitats of rare and endangered insects and other terrestrial arthropods, offers modest research grants to support scientific work which has some likelihood of contributing to the preservation of terrestrial arthropod populations as biological entities. Awards will usually be a few hundred dollars but may be larger if funds are available. Young workers and those without formal professional affiliation are encouraged to apply. For details, write to Dr. Francis Chew, Xerces Grants Committee Chairman, Dept. of Biology, Tufts University, Medford, Massachusetts 02155, U.S.A.

WANTED: Live Utetheisa ornatrix females, ongoing supply. Contact David Dussourd, 607-256-4464, Langmuir Lab, Cornell University, Ithaca, N.Y. 14850.

BIOLOGY OF BUTTERFLIES, ROYAL ENTOMOLOGICAL SOCIETY OF LONDON, 11th SYMPOSIUM, 22nd-25th SEPTEMBER 1981: The Society's 11th Symposium will be a four-day residential meeting to be held at the University of Reading. The programme will be concerned with ecology, population genetics and communication of butterflies.

This new style Symposium will comprise sixteen invited lectures; three sessions for discussion papers; exhibits; films and social events. The Convenors are R. I. Vane-Wright and P. R. Ackery, both of the Department of Entomology, British Museum (Natural History), London, S. W. 7, England.

Further details, including the registration forms and programme, will be distributed in the October issue of Antenna (c/o BMNH).

BIOQUIP: New catalog of entomological equipment now available. Substantial new material listed. Write: Bioquip Products, P. O. Box 61, Santa Monica, CA 90406, U.S.A., 213-322-6636.

EARLY STAGES: Purchase/Gift/Exchange---Eggs or pupae with foodplant material and data, all butterflies and large moths worldwide for research on culture methods. Minimum 2 dozen lots; write giving quotes if not a gift. We have substantial western America and Nepal specimens and some strains for exchange. R. H. T. Mattoni, Agresearch, Inc., 2130 S. Granville Avenue, Los Angeles, CA 90025, U.S.A., 213-479-8494 or A. C. Morton, 2 Barnes Street Cottages, Tonbridge, Kent, U.K. (073274) 256.

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