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## NOTES ON OVERLAPPING SUBSPECIES.

### I. AN EXAMPLE IN *SPEYERIA ZERENE* (NYMPHALIDÆ)

by L. P. GREY and A. H. MOECK

During the 1959 and 1960 seasons MOECK collected series of *Speyeria zerene* (Boisduval) in and near the Warner Mountains, Modoc County, California, demonstrating a geographical overlap of two radically different subspecies and thus reinforcing a hypothesis of relationship hitherto deduced more indirectly.

For background, illustrative material appended includes a resume (table 1) of subspeciation accredited to *zerene*, and a chart (map 1) indicating geographical distribution of the subspecific characters; these should enable orientation of the forms to be discussed herein. Topography of the particular areas mentioned is shown by map 2; specimens selected to depict normal and extreme variation in spot localities are illustrated in figures 1 and 2. The field notes on these series will be found appended, in a concluding section.

Figure 1 is of a series of males (in ventral aspect) from an unnamed ridge about 16 miles east of Eagleville, California, lying in Washoe County, Nevada. Normal variation in that locality is represented in rows 2 and 3 of figure 1, and is referable to the subspecies of *zerene* termed *cynna*. [Note: names considered lower-than-species are used throughout as catchwords; extent of blending discourages formal categorical applications.]

In a population of this sort, the upper singleton in figure 1 is remarkably abnormal, as would be more evident if seen in full color; it has well-developed ruddiness. The lower singleton has a reddish tinge; the specimens immediately above it (row 4) are largely unsilvered. Redness,

and lack of silver—these are characters unheard-of in *cynna* throughout the large area which that subspecies preempts in central and northern Nevada, in southern Idaho and southeastern Oregon. These two particular characters are, however, quite the normal thing in another *zerene* subspecies occurring just across the street, so to speak, from this Nevada colony.

Turning to figure 2, the three examples in the bottom row (M, N, O) will convey a good idea of normal *zerene* variation in the nearby Warner Mountains, i.e., running a bit darker but otherwise quite like the nominotypical Sierran forms. The remainder of the series in figure 2, namely, the sixteen specimens A through L in the four upper rows, are from the Patterson Meadows, at the southern end of the Warners in the southeastern corner of Modoc County. All were taken within less than a two-mile radius in substantially identical ecology and at about the same elevations (7300-7500 ft.).

Typical *zerene* predominated (samples G, H, I, L) but *cynna* also was procured here (samples A, B, J, K). Some individuals were strikingly intermediate (samples C, D, E, F) and all the more interesting since two (D, E) were in a "congregation of *cynnas*" and one (F) was in association with *zerene*. The greatest extremes (J and L) were netted from the same flower bed although in different years.

Attempts to secure large samplings were unsuccessful, being hampered by the aridity and lack of roads. The Patterson Meadows locality is the only one as yet discovered along the east rim of the Warners where this blending is widespread and obvious although occasional singleton intermediates have been taken in those mountains. Closer search was clued and encouraged by the gene recombinations noticed in the Washoe County series.

The rough balance of segregation vis-à-vis blending occurring in the vicinity of Patterson Meadows lends credence to a rather commonly held hypothesis, which is that the colonial and individual "pale *zerene*" turning up along the Sierran-Basin tension zone (the *malcolmi* near the Mammoth Lakes, the mixtures in the Tahoe passes, etc.) are resultants from contacts between the red Sierran and the yellow Great Basin forms. The relationships originally were deduced from cumulative gene replacements observable around a two-thousand-mile horseshoe (Moeck, 1957); present records serve to confirm opinions of the phylogeny as based on directions taken by variation in geographically arranged material. The extreme divergence of the end-products discouraged hope of ever finding intermediates; the segregation accompanying the blending is not at all surprising.

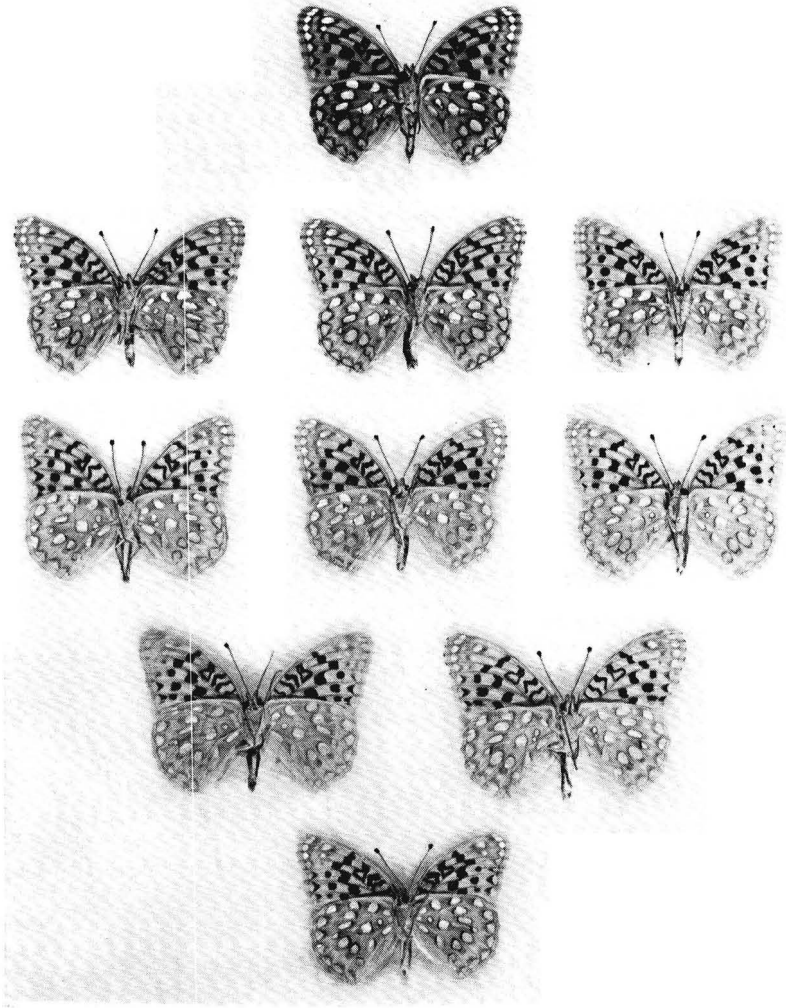


Fig. 1: Samples of *S. zerene* ssp. from Washoe Co., Nev. See locality on map 2, data in record section, comments in text.

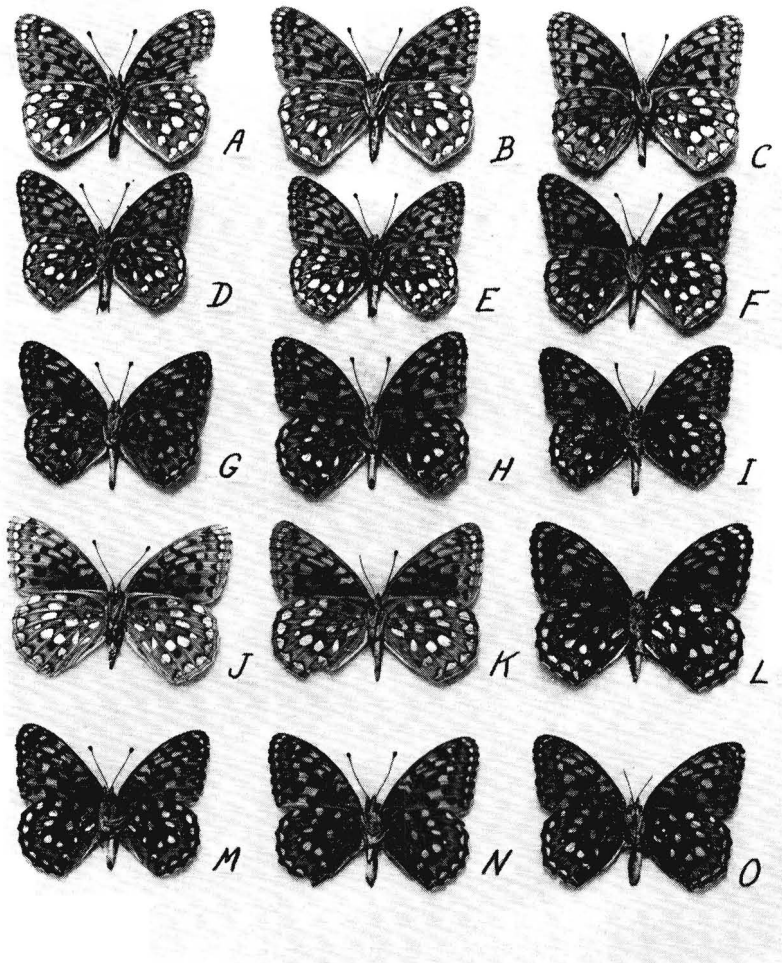
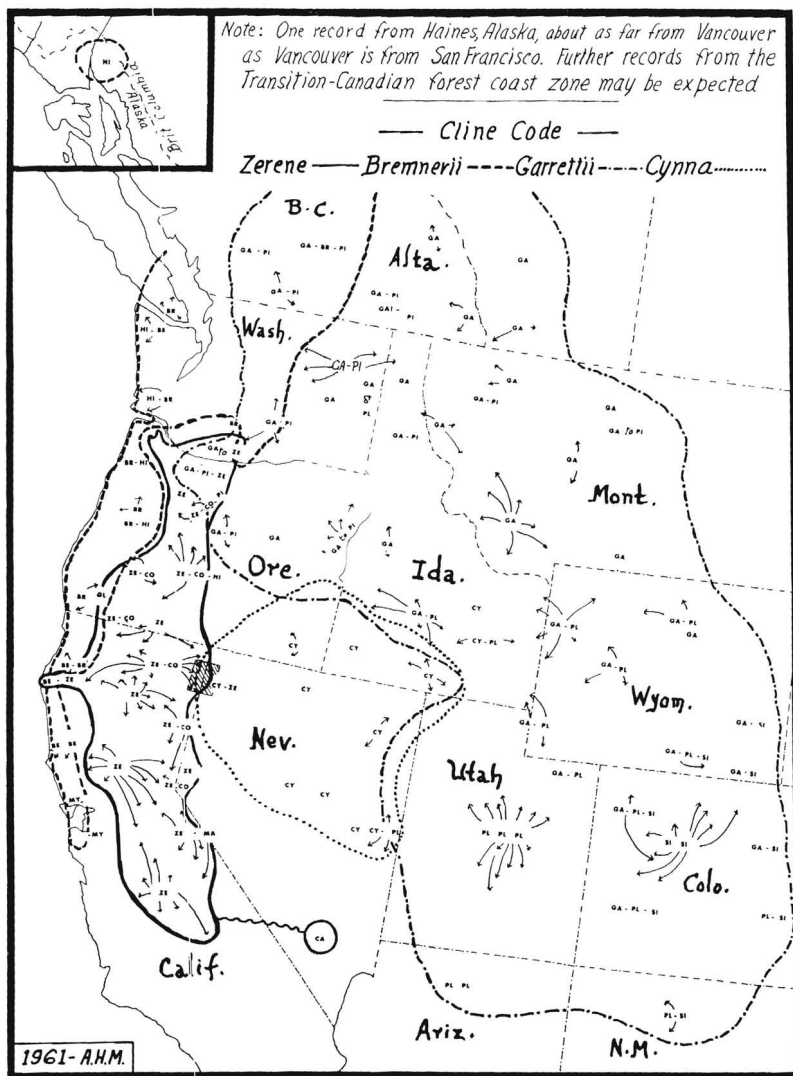


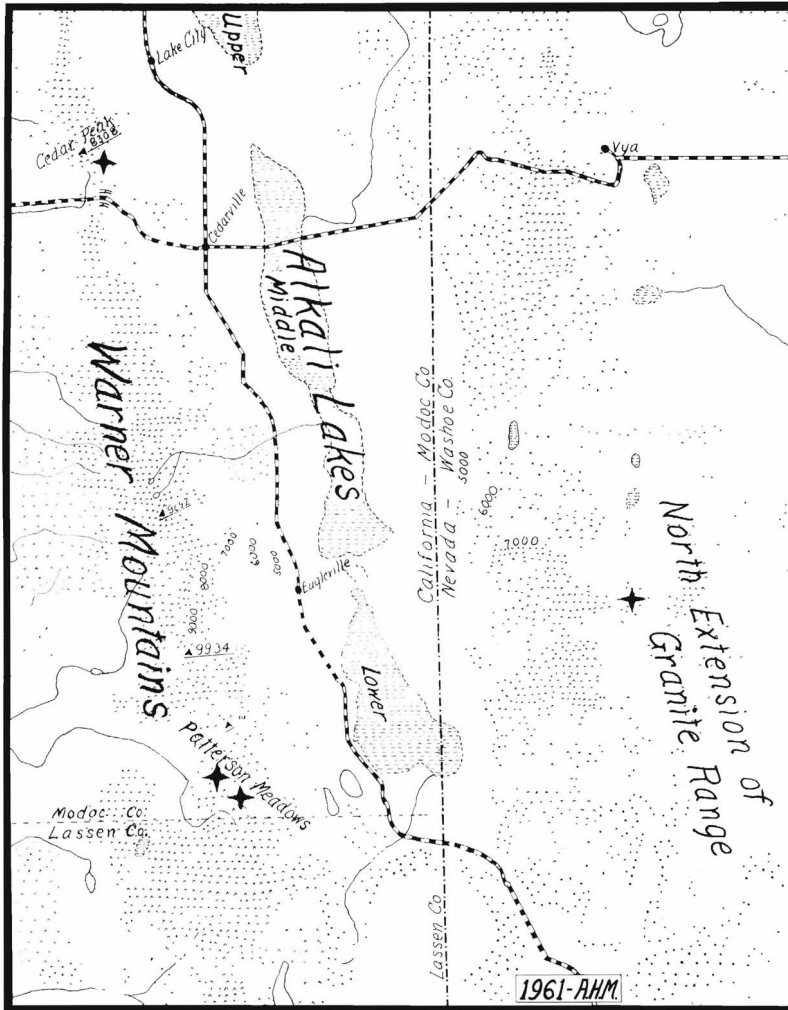
Fig. 2: Samples of *S. zerene* ssp. from Modoc Co., Calif. See localities on map 2, data in record section, comments in text.



Map 1: Distribution of *S. zerene*. See table 1 for key to symbols. The shaded rectangle denotes area shown in map 2.

## DISCUSSION

Mention of other geographically correlated peculiarities of *zerene* seems due, but is abbreviated because of a desire to expand some remarks on problems at which this and succeeding articles are aimed.



Map 2: Topography of a section of Modoc Co., Calif., and Washoe Co., Nev., where *S. zerene* ssp. illustrated in figs. 1 & 2 were taken. See record section and text comments.

For that matter, students familiar with Western topography and with *zerene* probably will find all of their observations and conjectures implicit on map 1. Appearing there, for examples, are (1) the gross correlations of the four large divergencies with the four physiographic provinces; (2) the zones of stability and instability – accordingly as clines converge or overlap, and with individual variation lessening

toward the middle and south portions of each province; (3) the hints of refugia, viz: (a) that the Coast Range set is incongruously largely divergent, possibly from an earlier archipelago, (b) that *platina* likely is nearest to the earlier "heartland" interior form, *garretti* a recent offspring wave northerly, *sinope* a Wyoming Basin isolate, *cynna* a relatively undisturbed Snake River Plateau resident, (c) that the southern distribution (as always) is the most obscure—is *carolæ* a relict, parent to Sierran forms, or a recent emigrant therefrom?—and why the hiatus in the Greenhorns and Tehachapi, the rarity in the Plateau country?—this insect demonstrates successes and tolerations to warrant some expectations which are disappointed southerly, so the failures probably have special significance; (4) the area of greatest plasticity, in the Pacific Northwest, as is inevitably predicted by the cornering of the four zones in that region and from the ideas of glacial retreat which indicate a recency of the contacts. Now, to the Modoc-Washoe County material: this, almost surely, exemplifies *intraphyletic segregation*.

Herein, and in following papers, the writers will point to instances, mostly in *Speyeria*, of apparent partial or total segregations occurring within the distributions of varieties presumed related to the extent of belonging to single phyletic lines—or, if defined in a quibbling spirit, belonging within a single "species" as best that category can be applied with present knowledge. Overlaps of this nature are engaging attention of researchers in a number of fields of evolutionary inquiry, for it is believed that such collisions of isolates are likely to provide rich data for genetical, cytological, paleogeographical and other studies.

Questions raised by these occurrences seem almost endless; some will be noted in later papers; in this discussion attention is drawn to three aspects, to wit: (1) the taxonomic, (2) the geographical (correlations with environment and barriers) and (3) the paleogeographical—which belongs closely bracketed with (2) because of uncertainties as to when the divergencies within population structures have been acquired.

Notations of overlaps such as these are obligations falling largely on taxonomists. It is they who presume to name and index species, from which listings the studies of evolution take their directions. Some of the conceptual modifications brought on by discoveries of taxonomists (*e.g.*, intraphyletic segregations—wherein species fragments differ to the extent of appearing locally discrete, and siblings—wherein convergence is uppermost, so that specific distinctness may be thoroughly masked, lying more in biology and behavior than in facies) obviously have affected evolutionary thinking. It is quite certain that more local anomalies of such caliber remain to be discovered, and that existing classifications will

Table 1. POPULATION STRUCTURE OF *SPEYERIA ZERENE*.

(On map 1, geographical areas of segregation and blending of these tabulated characters are shown by index symbols denoting the clines and subspecies as listed below).

| Symbol | Name                | Characters  | Distribution                             |
|--------|---------------------|---|--|
|        | CLINE 1             | DARK RUDDY ABOVE, DULL BRICK DISK, SORDID BAND                          | SIERRA NEVADA, SOUTHERN CASCADES         |
| ZE     | <i>zerene</i>       | silvering becoming absent southerly                                     | South to Middle Sierra Nevada            |
| CO     | <i>conchyliatus</i> | silvering & melanism increasing northerly, laps into clines 2 & 3       | Northern Sierra, Southern Cascades       |
| MA     | <i>malcolmi</i>     | paler, lighter band, mostly silvered, intergrades toward cline 4        | East Slope Sierra, Mammoth L.-L. Tahoe   |
| CA     | <i>carolæ</i>       | ruddy, but with yellowish cast, dull silver & band, an outlying isolate | Charleston Range in Southern Nevada      |
|        | CLINE 2             | RUDDY ABOVE, RED DISK, CONSPICUOUS YELLOW BAND, INVARIABLE SILVER       | PACIFIC COAST RANGES                     |
| BR     | <i>bremnerii</i>    | heavy dark pattern above, basal suffusion, limbal area lighter          | Puget - Willamette Trough, Ore. to B. C. |
| HI     | <i>hippolyta</i>    | small than <i>bremnerii</i> but similar in other respects               | near the ocean, Ore. to Alaska           |
| GL     | <i>gloriosa</i>     | intergrading from <i>bremnerii</i> to cline 1                           | interior coastal slope of so. Ore.       |



|    |                 |   |  |
|----|-----------------|---|--|
| BE | <i>behrensi</i> | lessened basal suffusion, browner disk, intergrading to cline 1       | No. Calif. coast, Mendocino Co., etc.        |
| MY | <i>myrtleæ</i>  | light ground, deep basal suffusion, a southernmost coastal divergence | Middle Calif. coast, Marin Co., etc.         |
|    | CLINE 3         | BROWNISH ABOVE, SILVER INVARIABLE, DISK SOME SHADE OF BROWN           | NORTHERN CASCADES, ROCKY MOUNTAINS           |
| PI | <i>picta</i>    | disk tending reddish, intergrading to cline 2                         | E. Slope No. Cascades & toward Rockies       |
| GA | <i>garretti</i> | brownish disk with some white flecking, narrowed band, good-sized     | No. & Middle Rocky Mts. foothills            |
| PL | <i>platina</i>  | tending smaller, paler, wider band, intergrading to cline 4           | Plateau, Basin, & edging the Rockies         |
| SI | <i>sinope</i>   | still smaller, sharpened pattern, brown to greenish disk              | N. W. Colorado & S. E. Wyoming               |
|    | CLINE 4         | REMARKABLY PALLID, PALE BUFF DISK NOT MUCH DARKER THAN YELLOW BAND    | UPPER GT. BASIN, SNAKE R. PLATEAU            |
| CY | <i>cynna</i>    | silver invariable, intergrades to clines 1 & 3                        | No. Nev., So. Ida., N. E. Calif., S. E. Ore. |

*Notes:* Available names ignored include (1) *sordida*: type locality questionable, hence useless as symbol of known local variation; (2) *pfoutsi*: needlessly fine splitting due to GUNDER's erroneous identification of *platina*; (3 & 4) *shastaensis* and *sineargentatus* represent aberrant individuals, not populations. Recognition of *cynna* as coequal with other regional groups follows from an assumption that it is descendent from a similarly major isolation. *N.B.*: the *myrtleæ* mapped below San Francisco Bay now is presumed extinct.

be set up by them. Evolutionary conceptions draw their warrants from the prevailing editions of "species"; taxonomy provides the impetus.

The *cynna* - *zerene* overlap falls within boundaries of credibility as established in the 1945 dos Passos and Grey catalogue of *Speyeria*, wherein *cynna* is listed as a subspecies of *zerene*. A regrettable error in that index is corrected hereby: the *carolæ* population in southern Nevada pretty surely belongs within *zerene* and not under *coronis* (Behr) where it was described originally.

Present taxonomic worries therefore seem unnecessary, except as all such relegations have to continue passing the yearly tests of new discoveries and changing concepts. The *Speyeria* classification mentioned was framed deliberately to reduce species to the utter minimum allowable against sympatrisms, allopatrisms and intergradings as then known. Future revisions probably will be more of concept than of groupings: it will appear that those who have catalogued *Limenitis*, for one example, make more species than the present speyerian philosophy would admit, and so it goes; in various genera some will lump, while others, familiar with the same data, will claim that lumping is not the best answer.

Some valuable taxonomic moralizings probably can be drawn from study of intraphyletic segregations within *Speyeria*; the situations described assuredly will be found duplicated, substituting places and species, in genera such as *Papilio*, *Euphydryas*, *Cercyonis*, etc., which seem now on the verge of long-awaited syntheses. It may be helpful to emphasize, as is the intention, that overlaps can be obscure in many ways and in sophisticated fashions, almost sure to be overlooked unless the fund of distributional knowledge is at once broad and detailed. Some hybrid zones shout their presence and are matters of common knowledge, as in Northeastern *Limenitis* and *Colias* — even then they may baffle taxonomists intent on pouring all of the new wine into the old skins of Linnaean concepts — but others may be entirely unsuspected because with data as skimpy as ordinarily is available the early stage of hypothesis would have to be made in defiance of the very cornerstone tenets of the species-makers, for these reasons:

The usual picture of subspecies is of geographically oriented divergencies which blend with other intraspecific forms along sharp or ill-defined boundary lines. But divergence in plastic genera can be extreme to the point of incredibility. Intergradings which would clue relationships may be slightly or not at all in evidence, perhaps confined to poorly explored areas or even lost by extinction. What, then, if two great extremes work into contact? Local samplings are likely to come up with two very different forms, each apparently discrete. By con-

ventional standards these indeed are species. Local naturalists must be allowed their word of truth: sympatry plus evident biogenetic differentiation spells out "species" quite positively. But students of population structures also have a right to be heard: if locally discrete sympatres display a gradual convergence when traced geographically into other regions, ending in an area or areas where blending is conspicuous or total, then a phyletic wholeness is manifested, which it is incorrect to claim for any of the parts.

Arguments and rebuttals of this sort will be heard increasingly as distributions are studied more intensively. Even now, the quirks of speciation and subspeciation known in butterflies compare favorably with those recorded for other groups of animals, and they will be scanned even closer in the future by students of evolution. Systematic taxonomy of butterflies therefore is in need of continued scrutiny; there are new frontiers; they lie, however, where they always have, *i.e.*, with segregations and overlaps. The concepts and tools need refining to deal with complexity hitherto suspected and now being confirmed.

A second arresting feature of intraphyletic overlaps, in addition to their challenges to taxonomy, are their morphological dissimilarities which so obviously flaunt the hypotheses built around ideas of variation responding to local ecogeographies. There has been a great deal of research along the latter lines, prompted by convergencies and parallels seen not only within closely related genera but also among forms known to be well apart phyletically. As an example of explanations which have been sought in particular factors of a shared environment the work by HOVANITZ (1941) is a classic of its kind.

Parallels within *Speyeria*, as noted by HOVANITZ, lend themselves irresistably to evolutionary speculations, being numerous to the point of endlessness, often involving very different species (and thus throwing heavier burdens on taxonomists quite sufficiently beset with anatomical likenesses and ecological overlaps). HOVANITZ's correlations of melanism with insolation stand unanswerable. He makes no further special claim that environment has the paramount role in determining variation, as some others have done with less excuse, or have so implied by pointing out the many geographically correlated parallels in various genera.

Recently (1959), VAN SOMEREN and JACKSON have summarized some ways in which parallels are supposed to evolve consequent from various kinds of mimicry, including *arithmetic mimicry* which certainly ought to apply in *Speyeria* to the advantage of locally scarce species; in these cases the convergence results from a "dwelling together" but has nothing directly to do with geography.

Such theories have the attraction of offering plausible rationalizations of wide applicability. They have a drawback of seeming to finalize "causes" which almost surely are incredibly multi-factorial however plainly one element may appear to stand out.

Dissimilarities evidenced in intraphyletic segregations give salutary check to environmental postulates. For example, *cynna* and *zerene* are at the very antipodes in coloration, and yet they face one another in similar ecologies across narrow barriers—and now turn out to fly in the same meadow. In such instances, it may be inferred that properties which are intrinsic (incompatibilities based in physiology) outweigh all extrinsic things such as geographical propinquity and identity of ecological background.

In a later paper attention will be directed to a segregation which really may have resulted in large part from differential adaptability to micro-environmental factors, as perhaps can be found upon close analysis in the other overlaps of isolates. Still and all, it hardly seems tenable to suppose that segregations such as in Appalachian *Limenitis* can be explained as being due to any sharp breaks in climate or ecology. There, and most likely in the great majority of overlaps, the better rationalizations seem to lie with genetics, with time, and with paleogeography.

The time element undoubtedly is the great enigma underlying the questions with which evolutionarily oriented taxonomy grapples. How long does it take, what particulars of environment are needed to cause species to diverge? Once established, how stable then are the gene systems thus integrated harmoniously to place, time and species? As the years bring changes, as populations migrate with climates, and as balances are struck between selection pressures and mutation rates, what then does local variation reflect of immediate situation and of earlier history?

A sharp dichotomy runs through the whole literature and theory of evolution: On the one hand, a multiplicity of "causes" are adduced which logically ought to lead only to chaos, the supposed mechanisms and modifiers being varied and acting at random; on the other hand, the natural order reflects crystallization into definite patterns down to such trivialities as that certain subspecies of butterflies occupy territory to the exclusion of others. Can it be that the "causes" by their very infinity give statistical expectation of orderliness in resultants, as in the modern "laws" of physics?

This touch of paradox is delightfully exposed in FORD's (1954) *Butterflies*, where mention is made of a strain of *Euphydryas* which was observed to subspeciate markedly in less than three decades—followed

later by a chapter discussing Pleistocene population movements as deduced (how else?) from present distribution of wing characters!

Observed population structures lend themselves to just such contradictory speculations, being (1) easily upset by outbreeding, population fluctuation or applied experiments, but at the same time (2) appearing in the wild state as geographically well-entrenched in respect to subspeciation, so that some form of selective elimination has to be postulated as operating to choke off blending observed to go on in contact areas.

It is easy, then, to deduce that variation is a reed in the wind, a pliant hostage to circumstance. But there is even more reason to postulate a really massive inertia inherent in population dynamics, as becomes almost a necessity when thinking over the history of systematic taxonomy. For example, as soon as continental glaciation moved up from theory to accepted fact, the large changes needed to incorporate arctic relicts on temperate-zone mountains were made without much argument, since affinities, when looked for, had remained very little obscured by those large isolations. In these and in similar instances taxonomists have had some conspicuous successes in equating classifications with earlier refugia and barriers, hence the growing tendency to suppose that paleogeography may be deduced in part from observed distributions, a hypothesis justifiable only if the rate of evolutionary change is quite slow.

In this connection, it is instructive to run through the data used by HOVANITZ in support of ecogeographic correlations: the idea of population movements and confinements underlying the observed regularities seems to appear equally valid; in fact, he was among the first to realize that local variation in *Speyeria* generally is predictable from surrounding character distributions. There is, then, no essential contradiction in the fact of intraphyletic segregates being so unlike although sympatric — these become comparisons in quite another dimension, namely, the one of time. The obvious correction is to allow for earlier isolations, granting that local effects of climates at best are a superimposition upon accumulated past heritage.

The present authors believe that intraphyletic segregations have their greatest interest in this suggestion that they probably are true signboards pointing to earlier isolations. If taxonomists succeed finally in defining species they will be in the same position as the pup that caught the locomotive: what to do with it? If it could be assured that wild populations tend to be reasonably stable in time — a proposition often taken for granted but by no means easy to prove — a fresh world

would open up for inquiry and distributional data could become a key unlocking new wonders.

Specialists in most groups already are convinced that morphology and biology provide insufficient criteria of specific discreteness and that some reckonings must be taken of paleogeography. The present authors will go so far as to suggest that degrees of divergency may be interpreted as providing fairly good indices of the degrees of isolation undergone by phyletic segregates. This would grant to evolutionary processes an evenness and inevitability not at all defensible, and to wing variation a long-term stability hardly in keeping with experience. It is seen, however, that *Speyeria* population structures fit with present ecogeographies in most details of clinality, but then show in zones of overlap degrees of segregation which accord roughly with estimates of earlier barriers and time scale, "as if" divergence were a function of time.

An example in the species *atlantis* (Edwards), typical of the untapped riches in *Speyeria*, demonstrates how overlaps can carry seemingly reliable indication of the durability of subspecies in time. An abstract follows:

An unusually ruddy and melanic population of *atlantis* occurs in the aridly isolated Stansbury Range, near the eastern side of the Great Basin in Tooele County, Utah. A very different (more pallid) *atlantis* occurs in line of sight, in the Wasatch Range, thus almost exactly paralleling the *zerene* - *cynna* confrontation. In this latter case, when the wing color characters peripheral to these colonies are mapped, and when the recent water and ice configurations (which here happen to be rather well known) are reconstructed, the character correlations all are with the late glacial geography and otherwise are worse than meaningless — the most like forms today are separated by the most tremendous barriers and the most unlike forms are in closest contiguity. The "small" barriers here are unusually formidable, so the argument can be made that sheer miles have nothing to do with the case — in fact, many people seem to think that divergence in isolated colonies such as are in the Stansburys is all a matter of local option and chance. Against this, the bulk of Great Basin distributions are roughly homogeneous despite scores or hundreds of dry valley barriers as severe as the ones between the Stansburys and the Wasatch Range; specialists note similar large regularities in population structures which hardly are in keeping with the idea of random subspeciation; the exceptions generally may be suspected of carrying special meanings, as in the presently cited instance where the integrating considerations clearly lie in paleogeography.

Very few distributions can be analysed as closely as would be possible with these colonies, to show that the Wasatch (recent intrusion) and the Stansbury (relict) populations are from different refugia. Present similarities of environment patently have not softened these divergencies; intermediates, such as occur, are found mostly in territories edging the foci of divergence, hence appear due to gene exchange through straying.

Surrounding variation gains rationality from the refugia suggested by this distribution. Students have only to look at a topographic map and subtract a few thousand years — then they will see grasslands and forests arising around the western rim of old Lake Bonneville, extending up through the “antelope country” of southern Idaho, and will see mountain glaciers creeping back over the Wasatch-Uinta highlands. The facies of the northerly “*tetonia*” then stands illuminated by the Stansbury discovery; the southwestern affinities of “*wasatchia*” then can be related to its recent entrance into a previously inhospitable upland; the present segregation then is unusually good evidence that the ephemera of wing colors are not to be shrugged off as local products of recent environments.

An example from another genus: *Lycæna* “*claytoni*” on shrub *Potentilla* in old fields, vicinity of Springfield, Maine, is widely different from *L. “dospassosi*” on a small prostrate cinquefoil in a salt marsh at Bathhurst, New Brunswick. Airline separation is about 300 miles, topographic barrier nil, ecologic barrier complete since neither foodplant is known from the intervening country. The Maine colony falls in a series having like facies and habits, distributed through Quebec and Ontario to Wisconsin and Michigan. The Bathhurst colony alone is anomalous. If specialists are correct in regarding all of these as biological radiates of a single phyletic line (the *dorcas* - *helioides* set), how is this distribution to be rationalized?

Nothing the simplicity gained by mapping the Maine-Michigan series as an outflow from a Mississippi Valley refuge, the incongruity of “*dospassosi*” then will recall that botanists and others report analogously queer isolates in and near the St. Lawrence Valley. The hints are of a separate East Coast (Grand Banks?) glacial refuge. This *Lycæna* segregation then would align with the idea herein stressed that such juxtapositions probably have their best explanations in paleogeography.

A fairly coherent synthesis of *Speyeria* can be achieved through this philosophy of regarding divergence as a function of geography and time. The practical aspects seem inexhaustable: good results continue to follow from adopting the catchphrase that geography can be trusted to produce specimens to order, and conversely, that specimens will reveal

geography, as would be demanded if equating present variation with paleogeographic refugia, for unless wing characters demonstrate (1) sensitivity to geography and (2) stability during local isolations, paleogeographic speculations would lack the necessary correlation with reality. These somewhat contradictory demands seem to be met by observed subspeciations: the degrees of segregation and blending usually accord with the constructions of landscapes and time.

As an example of specimens revealing geography, Mr. STERLING MATTOON (*in litt.*) recently found Lower Cascade - Sierran characters in a Coast Range colony of *zerene*, near Ferndale, Humboldt County, California. Upon inquiry as to possible ecological linkages which might rationalize this otherwise incongruous blending, he states that a yellow pine forest, a suitably indicative continuum, may be traced from near the coast here, following valleys into the Trinity - Shasta uplands.

As to the possibility of invoking geography to produce specimens, MOECK's explorations in the area shown on map 2 were centered there deliberately and with some expectation of finding mixed populations. A far cry, this, from the day when a red speyerian in a yellow population would have been one more incomprehensibility to place at the door of Chaos, this bee-line to a place designated, to search for the unknown postulated in advance!

It is no credit to the occult powers of specialists that they often seem to know where to look for particular character combinations; rather, it is a matter of projecting known population structure on a known landscape and then interpolating resultants. The credit obviously belongs to some large invariability in nature, which the present authors believe to be the degree of population stability required when postulating correlations with paleogeography. If more assurance is needed, the best things to regard are the impossibilities and contradictions arising when trying to correlate intraphyletic segregations with present environments.

Further illustrations, of commonplace and unusual variation equated to the theme of divergence harmonious with present and assumed past isolations, will be given in subsequent papers. It may be difficult to promote the idea that the supposedly unstable wing characters should have evolved in a fashion apparently providing *an analogue to the wanderings of the insects*. This, however, seems to be safer to defend, looking to samples of wild populations, than alternative propositions such as would associate subspeciations either with particular causes or with no causes at all; the fear that variation is mainly at random is wearing away, while older theories of adaptation to local climates are meeting increased questioning.



## RECORDS

[Map 1 was collated from records of approximately 3,000 specimens of *zerene*, abstracted from the senior author's card file of *Speyeria*. Students needing distributional data are welcome to borrow from these indexed records and are urged to contribute to their expansion.]

The specimens illustrated in figures 1 and 2, taken in the area shown on map 2, are out of batches with field notes as follow:

NEVADA: WASHOE CO.: "59BP": app. 16 mi. E. of Eagleville, Calif., in a patch of greenery on an unnamed, barren, dry rocky ridge (No. Granite Range outlier?), 7500 ft. elev., across the alkali lake from the Warner Mts., 17.vii.59 (*leg. MOECK*), 32 males near *cynna*, in good condition. The series includes 1 very red and 2 nearly unsilvered individuals. "59BQ": same place and date as 59BP but at 6800 ft. on barren rocks, 1 male *cynna*, a stray from the 7500 ft. elev.

CALIFORNIA: MODOC CO.: "60BD": E. side of Cedar Peak, N. of Cedar Pass, Warner Mts., 6500-7500 ft. elev., dry logging road through lightly forested hills, 22.vii.60 (*leg. MOECK*), 6 males, silvered and unsilvered, near Sierran *zerene*. "59BR": Patterson Meadows, app. 16 mi. S. W. of Eagleville, 7300 ft. elev. in brushy clearings along a creek, 17.vii.59 (*leg. MOECK*), 2 males, 1 female near *cynna*. "60BB": same place as 59BR, 21.vii.60 (*leg. MOECK*), 4 males and 1 female *zerene* ssp., the female brightly silvered, very red, the males from dull red to nearly as pale as *cynna*. "60BC": Middle Fork Spring of East Creek, about 2 mi. S. E. of Patterson Meadows in similar ecology along a creek, 7500 ft. elev., 21.vii.60 (*leg. MOECK*), 4 males and 1 female *zerene* ssp., 2 males red, remainder intermediate to *cynna*. Deposition: Collection of the junior author.

## ACKNOWLEDGMENTS

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## References Cited

- dos Passos, C. F., & L. P. Grey, 1947. Systematic catalogue of *Speyeria* (Lepidoptera, Nymphalidae) with designations of types and fixations of type localities. *Am. mus. novitates* 1370: 30 pp.
- Ford, E. B., 1945. *Butterflies*. pp. xiv + 358, 48 pls. (colored), 24 figs., 32 maps, 9 diagrams, 8 tables. The New Naturalist Series, Collins Press, London.
- Hovanitz, W., 1941. Parallel ecogenotypical color variation in butterflies. *Ecology* 22: 259-284.
- Moeck, A. H., 1957. *Geographic variability in Speyeria. Comments, records and description of a new subspecies*. 48 pp., 2 pls., 7 maps. Privately printed, sponsored by Milwaukee Ent. Soc.
- van Someren, V. G. L., & T. H. E. Jackson, 1959. Some comments on protective resemblance amongst African Lepidoptera (Rhopalocera). *Journ. lepid. soc.* 14: 121-150, 10 pls.

(LPG) Rt. 1, Box 216, Lincoln, Me., U. S. A.

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