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GEOGRAPHIC SUBSPECIATION IN THE LEPIDOPTERA

A Symposium

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I. Introduction: A GENERAL OUTLINE OF SUBSPECIATION

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Our meeting this afternoon is for the purpose of examining the geographical subspecies concept as applied to the Lepidoptera. I shall try to set forth some of the general theoretical aspects of subspeciation now widely accepted among modern systematists and evolutionists. The major portion of the symposium will be devoted to the presentation of the subspeciation phenomena found in each of the several faunal regions or taxonomic groups, by five Society members who are authorities on subjects on which they will speak.

Most of us here today are best acquainted with North American butterflies and moths, and most of us are familiar with the existence of geographic subspecies. Some of these subspecies are strikingly unlike, such as the Floridian and the northeastern races of *Limenitis archippus* (Cramer), the Viceroy, or the eastern and western races of *Pachysphinx modesta* (Harris), the big Poplar Sphinx Moth. Some are conspicuously unlike in one sex, for example, the northern and the southeastern races of *Papilio glaucus* (Linné), the familiar Tiger Swallowtail [see fig.1]. But the differences are usually more subtle.

First, it is necessary to state clearly that A SUBSPECIES IS A POPULATION, NOT AN INDIVIDUAL. Since a matter of considerable practical importance to us is the process of applying a name to any specimen we may have, the population concept finds us in an occasional awkward spot. Returning to the Tiger Swallowtail, we find that in the Arkansas population the female is characteristically blackish and that in the Massachusetts population the female is characteristically like the male (yellow with black lines). I believe that this dark female form will be found to be controlled by a single gene (pair of alleles). In Arkansas, if we rear adults from many female larvae, perhaps a few of them will emerge as yellow-and-black adults. A question is, can we call those few: "subspecies *turnus*", like the Massachusetts females which they closely resemble? And the answer must be, NO. For a clear designation we could refer to the two female forms in Arkansas as "*Papilio glaucus glaucus* yellow female"

and "*Papilio glaucus glaucus* dark (or normal) female". Then a dark female in Massachusetts which was known to be native (and not an immigrant from the South or an offspring of such an immigrant) would be designated "*Papilio glaucus turnus* dark female". A clarifying point in this case is that a block of ten males from Arkansas and a block of ten from Massachusetts, collected at random, can be distinguished rather readily when studied as series. If we rear male offspring of our Arkansas yellow female, they will be clearly of the Arkansas type, and if we rear males from the Massachusetts dark female, they will be clearly of the Massachusetts type. SUBSPECIES DIFFERENCES, LIKE SPECIES DIFFERENCES, ARE A COMBINATION OF SEVERAL CHARACTERS, not just one, although one character will often suffice for rapid identification.

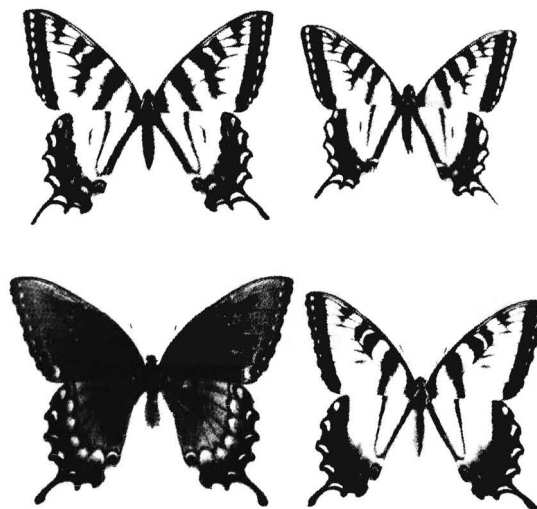


Fig.1. *Papilio glaucus* L.,
subsp. *turnus* above, subsp. *glaucus* below
(♀ on left, ♂ on right).

It should be added that in Missouri, Maryland, and other middle states, the two female forms are present in nearly equal numbers. Furthermore, the males fall between the northern turnus and the southern glaucus. There is a rather even gradient both in the percentage of the female forms and in the less conspicuous differences seen in the males. The point at which we draw the line between glaucus and turnus is purely arbitrary and thus a controversial matter. However, a very convenient method has been proposed by Huxley to deal with the even trend from one subspecies to another. He calls the steady trend a CLINE and the intermediate POPULATIONS not readily referable to one of the two subspecies names are designated with a "Cl.", followed by the names of both subspecies, hyphenated. Using this system, we would refer to the populations from the District of Columbia or central Illinois as: "Papilio glaucus Cl. glaucus-turnus".¹

A second generalization, which proceeds logically from the preceding definition of a SUBSPECIES AS A POPULATION, is that MOST, IF NOT ALL, SUBSPECIES ARE IN FACT GEOGRAPHICAL; that is, no two subspecies are permanent residents in the same locality. For Lepidoptera, foodplant subspecies have been claimed to exist, by various authors. In most, if not all, cases of reported ("sympatric") so-called "foodplant subspecies", they are probably two distinct species and hybridize little if at all. Examples are Franclemont's Symmerista leucitys on Maple vs. S. albifrons (J.E. Smith) on Oak, and Rawson and Ziegler's Mitoura hesseli on White Cedar vs. M. gryneus (Hübner) on Red Cedar. We can say that NO TWO SUBSPECIES PERMANENTLY OCCUPY THE SAME LOCALITY, for a fundamental reason, namely that a characteristic of subspecies is that they can and will intermate and produce fertile offspring if given the opportunity, whereas species rarely intermate at all and when they do, fully fertile offspring cannot result. From this it follows that if two subspecies did co-exist they would intermate so freely that differences would disappear and soon only one subspecies would occupy the region.

It must be noted, however, that two or more different subspecies may be found in one locality on rare occasions, but only one is the permanent and abundant resident of the locality; all others are immigrants whose characteristics are not successful in the locality invaded and therefore disappear quickly.

The third major principle I want to consider may be shown by describing ONE POSSIBLE MANNER OF ORIGIN OF SUBSPECIES AND SUBSPECIFIC DIFFERENCES. Although the general PROCESS on continental land masses is probably similar to this, the EVENTS may differ greatly.

Let us try to imagine the likely situation for one species when the last great Pleistocene glaciation had reached its southernmost limit. The plants very near the ice were lichens, a few sedges, grasses, dwarf willows, and other plants we now find only

in the Arctic or on mountain tops. Then came a broad band of spruce, lodgepole pine, aspen, and other plants now found in much of Canada and below timberline on mountains. Third came a broader band of hard maple, hemlock, birch, ash, yellow pine, and other plants now found in the northern States and at medium levels on mountains. Each of these bands was limited primarily by the temperature range and level (suppose that the temperatures in the lichen band ranged usually from -60° F. to +50° F.; in the spruce band from -20° F. to +70° F.; and in the maple band from -10° F. to +90° F.). Now suppose that the single species of Lepidoptera whose subspeciation we are following was restricted to the spruce-aspen band by temperature-tolerance limits, but that it further required a certain wild cherry for foodplant and could survive only where the humidity never dropped below 50% for more than a few days. At the time of greatest extent of the ice all these requirements were met throughout the whole temperature band, from the Atlantic coast to the Black Hills, and over most of the region to the west in which there were only separated mountain glaciers but where conditions were profoundly controlled by the presence of the great ice mass [fig.2].

As the world climate became warmer and the ice was steadily melted on its southern edge, the temperature bands were of course shifted steadily northward. In this process our Lepidopteron on the southern edge was being exterminated, but it was able to occupy new territory on its northern edge. Gradually, irregularities in the terrain were revealed as the ice sheet dwindled, with newly re-exposed mountains, valleys, and basins creating air-currents which changed markedly the rain and snow-fall in their vicinity. Broad arid zones appeared which were uninhabitable for our species and left its populations extending southward in tongues and bulges. In the mountains the species moved steadily up the slopes as the climate became warmer and warmer. In flatter terrain the species merely moved northward, leaving no southern remnant. Also, in mountains too low or too southern the necessary temperature band moved right up above the mountain tops, and the populations of our species disappeared there. Some of the sufficiently high mountains would of course be rather isolated loops without continuity to the next loop. Thus, isolated but thriving populations of our Lepidopteron would be left behind. [See fig.3] I will not continue this step-by-step treatment here, but you can easily see the course leading to the situation we would find today, which I can roughly outline as follows:

The temperature band now exists at sea level across central latitudes of eastern and western Canada and is found on a few mountain areas of the Appalachian chain, down the center as far as northern Michigan and Minnesota, and right down the Rocky Mts. into New Mexico and down the western cordillera to central California, and with very isolated populations in high ranges like the Wind River Range, the Rabbit Ears Range, the Grand Mesa, the Wasatch Mts., and so on (fig.4).

We can thus see how our species may have attained its present interesting distribution. There are very many species with such ranges, examples being Pieris

1. See also the articles by Kiriakoff and Remington in the Lep. News, vol.2: pp.3-4, 15, 16; 1948.

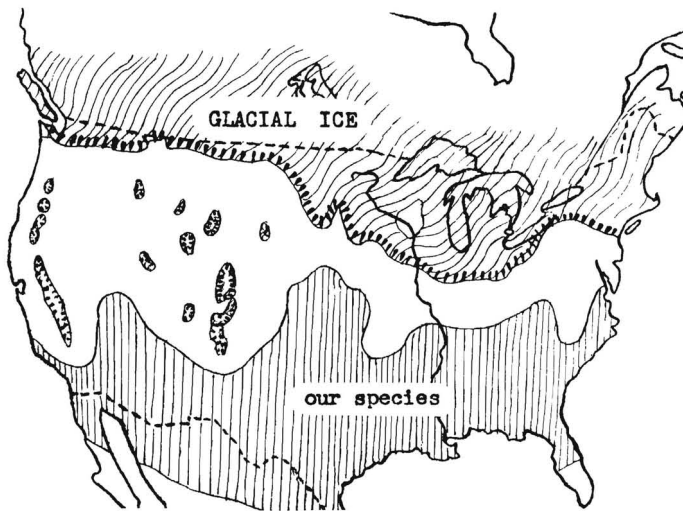


Fig.2. Last Glaciation at Maximum Limit.

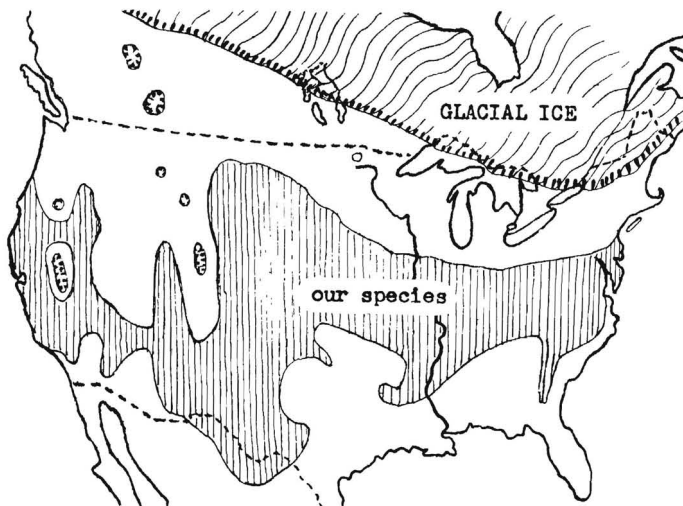


Fig.3. Glaciation Receding.



Fig.4. Present Conditions.

nadi (L.), *Pyrgus centaureae* (Rambur), the *Colias interior* Scudder group, *Glaucopsyche lygdamus* (Dblly.), *Celerio galii* (Rott.), *Arctia caia* (Linné) and so on.

Now the question arises as to how the subspecific differences appear in these populations, differences which allow us to recognize the populations by wing markings and other less obvious characters.

Each of the populations of a species is in somewhat different environmental conditions, and the more carefully we study them IN THE FIELD, the more obvious these differences become. The Wasatch Mts. may have generally pale rocks and soil while the nearby Rabbit Ears Range may have very dark rocks and soil. How does the Rabbit Ears population of our imaginary species become dark like the substratum, and how does the Wasatch population become pale like its substratum?

Suppose that our species arrived in these two ranges with a generally gray color and its main enemies were birds or mammals which depended on sight to catch the Lepidopteron. Mutations of its genes (the hereditary controllers which I have no time to explain here but which are clearly treated in E.B. Ford's *Butterflies**) are random and therefore presumably produce, in both the Wasatch and Rabbit Ears populations, individuals which are black and individuals which are white. The original grays are more easily seen than the blacks on the dark rocks of the Rabbit Ears Range. Therefore, each of these new blacks has a better chance of escaping and producing offspring than does any of the grays, and the percentage of blacks will rise steadily in each succeeding generation until the original gray type has virtually disappeared. In contrast, all the new whites will be even worse adapted than their gray and black brethren and will be eliminated by natural selection whenever they appear.

The reverse will of course be true in the Wasatch Mts., where the new whites will eventually eliminate the original group and the new blacks will always be quickly lost.

By this process, which I have of course vastly over-simplified, we now have a generally gray species found over a wide range, but with a black subspecies in the Rabbit Ears Range and a white subspecies in the Wasatch Mts., all three types now equipped with concealing coloration in their respective regions (Fig.5).

(continued on next page)

* 368 pp., 58 pls. (34 col.), published by Collins, St. James Place, London, England, and obtainable from them, or through most bookstores. [See review in *Lep. News*, vol.1: p.3; 1947.]

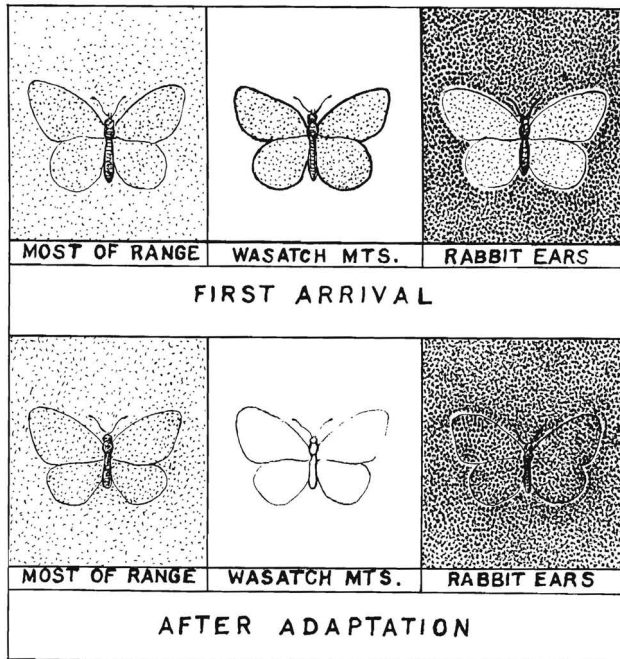


Fig. 5.

One last theoretical point I want to make concerns THE FATE OF THESE GEOGRAPHIC SUBSPECIES. A widely accepted view today is that species always arise from subspecies. This means that subspecies are potential species. The sterility barrier which we expect between species, with the correlative lack of successful hybridizing, is the result of an accumulation of a large number of genetic differences, not only of color as in the Wasatch and Rabbit Ears subspecies, but also of structure, flight habits, courtship patterns, tolerances of temperature, light, wind, and humidity, and in many cases foodplant differences. These differences must accumulate during a long period of isolation. Otherwise, too frequent interbreeding with other populations will continually dilute out the differences. Thus, a subspecies may become completely isolated for a long time from all other populations of the parent species and eventually become a distinct species, or the isolation may not be complete enough or for a long enough time and the subspecies will remain rather similar to other subspecies or may even lose its identity entirely.

Please let me emphasize that my main examples have been hypothetical and were concocted to help me explain theoretical points. No real examples from the Lepidoptera have been followed far enough to prove these points, although other organisms have been so studied.

II. SUBSPECIATION AMONG SPHINGID MOTHS OF THE WEST INDIES

by Margaret M. Cary

Mt. Airy, Philadelphia, Pennsylvania



Map of the West Indies

I must speak of this as an introduction to the study of subspeciation among Sphingidae of the Antilles because very little has been done along this line in any of the West Indies. Many collectors have worked there, and it is one of the very oldest collecting localities. These collectors and taxonomists have noted the many subspecies found in these subtropical islands but little work has been done

with environmental differences, with rearing of subspecies, with foodplant specialization, or with the causes of geographic subspeciation in the Islands, ideally situated though they are for such a study. Here we find small isolated populations and a most interesting geologic history. The island called Hispaniola, which is divided politically into Haiti and Santo Domingo, has been much neglected even by collectors, and the island of Puerto Rico has been so denuded of original vegetation, including its former magnificent forest cover, by an ever-increasing population of impoverished inhabitants, that any comparison of present subspecies with past populations is regrettably uncertain.

In speaking of Antillean subspecies of Sphingidae I am speaking only of those endemic to the islands. To illustrate this: - *Erinnyis lassauxi omphaleae* (Bdv.) and *Erinnyis lassauxi merianae* (Grote) are found on the islands, but both occur on adjacent continental areas. As far as is now known we have 32 subspecies of Sphingidae on the Greater and Lesser Antilles and let me state here very clearly that the island of TRINIDAD IS NOT ONE OF THE ANTILLES but a part of the continental shelf of South America.

In this paper I am following Ernst Mayr's defin-

SUBSPECIATION SYMPOSIUM. Cary: West Indian Sphingidae - cont.

ition of a subspecies, found on page 106 of his book, *Systematics and the Origin of Species*: "The subspecies or geographic race is a geographically localized subdivision of the species which differs genetically and taxonomically from other subdivisions of the species." In dealing with subspeciation we find two processes involved, the development of diversities, and the establishment of discontinuities. The Antilles are admirably suited to a study of subspeciation of Sphingidae through geographic isolation, because here we are dealing with small populations isolated from parental groups and developing as races which because of localized foodplants tend to become sedentary and restricted; with repeated invasions in some cases; and with certain moths more given than others to variation, exhibiting diversity in pattern, color, size, etc., probably attributable to processes of natural selection.

I have chosen for special discussion eight Antillean subspecies of Sphingidae, because several of these eight have the nominotypical race endemic to the Antilles, because some of these eight have a marked tendency to variation, because some of them seem to illustrate the theory of successive immigrations to the islands, and because some of them lend themselves to interesting comparisons with similar species not only on adjacent continental areas but with those on our only Western Hemisphere group of islands comparable to the Antilles, the Galapagos Islands. *Phlegethontius sextus*, the common Tobacco Moth of North America and Mexico, is represented on the Greater Antilles (Cuba, Jamaica, Puerto Rico, and Hispaniola) by race *jamaicensis*, differing mainly in its greater average size, in its brownish tinge, in its clouded white bands of the lower wing and in slight differences in the genitalia. On the Lesser Antilles, especially on the islands of Dominica and St. Lucia is found the much smaller, more monotonously colored race, *lucia*, with bands on the hind wings pure black and white. On Trinidad, which is part of the Parian Shelf of Venezuela, we have the South American subspecies *paphus* (Cram.). I feel that geographic isolation is the cause of subspeciation here. Various members of the Nightshade family (Solanaceae), on which the larvae of *sextus* feed, are distributed through North America, Mexico, Central and South America, and the Antilles. There seems no evidence here of adaptive evolution since foodplants, predators, and parasites, and general habitat conditions are similar in all of the Caribbean islands. *P. sextus* reached the islands long ago geologically, probably after the Miocene submergence of all but the highlands of the Greater Antilles, and has evolved separately because of isolation. However, *Phlegethontius rusticus* is, I think, illustrative of different invasions, some of which are probably continuing today. The parent form of *rusticus* occurs in North and South America, Mexico, Trinidad, Jamaica, Puerto Rico, and Haiti, as well as in Cuba along with *P. rusticus cubanus*, a smaller brown form with the brown discal area of forewing spread to the outer margin of forewing. *P. rusticus* occurs in Haiti along with a large and striking narrower-winged subspecies, very black and handsome, called *dominicanus*. The subspecies of the Lesser Antilles called *harterti* is like the nominotypical *rusticus* except that the dark costal marginal tri-

angle is very light. *P. rusticus postscriptus* (Clark) is found on the Galapagos Islands and it may well be that *Phlegethontius nigritus* (R. & J.), found there also, traces its long descent from *rusticus*, though here we find a slight change in the wing-shape. In *P. brontes* we have a very variable moth whose nominotypical race is in Jamaica and exceedingly common. Its foodplant is the yellow-flowered *Tecoma stans*, quite abundant on the Greater and Lesser Antilles. The Cuban subspecies, *cubensis*, is smaller and less strikingly marked, and has probably been blown to Florida in hurricanes, since we have caught it there over petunias at dusk at Everglades. It is certainly scarce in Florida and I think also in Cuba. It probably feeds on another member of the Bignoniaceae in Florida, as *Tecoma stans* is not in Florida. In Haiti *P. brontes haitiensis* is very common and is the black and white form of this insect. Puerto Rico has the more creamy brown subspecies *mythi*, a large, handsome insect but apparently scarce.

We now come to *Isognathus rimosa*, one of the species which gives rise to at least eight genitally distinct subspecies in the Antilles and adjacent continental areas, as well as probably two very constant forms in Cuba which may well be overlapping ends of circles. *Isognathus r. rimosa* occurs apparently only on Cuba, where we also have two most interesting forms, sometimes listed as subspecies. *I. rimosa congratulans* Grote & Rob. and *I. rimosa woodi* Ramsden. Dr. Karl Jordan, of Tring, believes these to be forms of *rimosa* rather than subspecies and since two subspecies of the same species do not co-exist as separate entities in the same locality, rather tending to intergrade, we shall call them forms. But much more study must be done here in Cuba as to the definite geographical locations of these two forms, their foodplants, etc. In appearance *congratulans* has the same tan color as subspecies *rimosa* but lacks the characteristic trapezoidal black marking on forewing. *I. r. woodi* is remarkably different looking, a clouded black and white insect, rather ghostlike in appearance and very striking, really resembling its parent form only in its striped body. In Jamaica we find the large and handsome subspecies *jamaicensis*, of which there are only the following specimens recorded in collections: - one at the Carnegie Museum, Pittsburgh (Collection Holland, Oberthür, Clark); one at the Institute of Jamaica in Kingston; and one in the private collection of Bernard Heineman. In Hispaniola we have *I. rimosa molitor* which appears to be quite abundant there and is a handsome whitish insect. In Puerto Rico there is subspecies *walcotti*, differing from other subspecies of *rimosa* on the Islands by having a much narrower black band on the hind wing, the ground color here being brownish as in *I. r. rimosa* and *I. r. jamaicensis* instead of white as in *I. r. molitor* and the continental *I. r. papayae*. It seems a connecting link among the subspecies of this variable insect. Subspecies *papayae* is also in Trinidad, and *inclitus* in Mexico, while other subspecies of *rimosa* are in Brazil and other parts of South America.

Pachylia syces syces is found in Mexico and Central and South America, though in my long collecting experience nowhere as common as *P. ficus*. In Jamaica

SUBSPECIES OF SPHINGIDAE ENDEMIC IN THE ANTILLES					MEXICO AND CENTRAL AMERICA
JAMAICA	CUBA	HISPANIOLA	PUERTO RICO	LESSER ANTILLES	
<u>COCYTIUS</u> <u>vitrinus mus-gravi</u> Clark	<u>v. vitrinus</u> R.&J.				<u>PHLEGETHONTIUS</u> <u>occultus pacificus</u> Mooser <u>hannibal mayeri</u> Mooser <u>lucetius nubilus</u> R. & J. <u>lefeburei bos-sardi</u> Gehlen <u>floristan cab-nal</u> Schaus <u>floristan ish-kal</u> Schaus <u>crocala tepici</u> Clark
<u>PHLEGETHONTIUS</u> <u>sextus jamaicensis</u> Btlr.	<u>sextus jamaicensis</u> Btlr.	<u>sextus jamaicensis</u> Btlr.	<u>sextus jamaicensis</u> Btlr.	<u>sextus lucia</u> Gehlen	<u>lucetius nubilus</u> R. & J. <u>lefeburei bos-sardi</u> Gehlen <u>floristan cab-nal</u> Schaus <u>floristan ish-kal</u> Schaus <u>crocala tepici</u> Clark
<u>r. rusticus</u> Fab. (not endemic)	<u>rusticus cubanus</u> Wood	<u>rusticus dominicanus</u> Gehlen [<u>r. rusticus</u> Fab. also is here]	<u>r. rusticus</u> Fab. (not endemic)	<u>rusticus harterti</u> Rothsch.	<u>NANNOPARCE</u> <u>poeyi haterius</u> Druce
<u>b. brontes</u> Dru.	<u>brontes cubensis</u> Grt.	<u>brontes haitiensis</u> Clark	<u>brontes smythi</u> Clark	<u>brontes</u> in some form probably on L. Antilles since foodplant (<u>Tecoma</u>) there	<u>SPHINX</u> <u>libocedrus achotla</u> Mooser <u>separatus mel-aena</u> R. & J. <u>chersis mexicanus</u> R. & J.
<u>AMPLYPTERUS</u> <u>gannascus jamaicensis</u> R. & J.	<u>gannascus cubanus</u> R. & J.			<u>afflictus bahamensis</u> (one specimen only)	<u>AMPLYPTERUS</u> <u>donyza dariensis</u> R. & J.
<u>ISOGNATHUS</u> <u>rimosa jamaicensis</u> R. & J.	<u>r. rimosa</u> Grt. (and <u>congratulanus</u> and <u>woodi</u> ? see text)	<u>rimosa molitor</u> R. & J.	<u>rimosa wolcottii</u> Clark		<u>SMERINTHUS</u> <u>cerisyi saliceti</u> Bdv.
<u>ERYNNIS</u> <u>obscura jamaicensis</u> Clark				<u>obscura stheno</u> Hbn.	<u>CALASYMBOLUS</u> <u>myops macrops</u> Gehlen
<u>domingonis pallescens</u> Clark					<u>ISOGNATHUS</u> <u>rimosa inclitus</u> Edw.
<u>PAGHYLIA</u> <u>syces insularis</u> R. & J.	<u>syces cubensis</u> Closs			<u>PERIGONIA</u> <u>*lusca major</u> Clark <u>*lusca bahamensis</u> Clark	<u>ERINNYIS</u> <u>obscura socorrensis</u> Clark
<u>SESIA</u> <u>tantalus eumelus</u> Jordan	<u>titan cubensis</u> Clark				<u>HEMEROPLANES</u> <u>pan denticulata</u> Schs.
<u>PHOLUS</u> <u>s. satellitia</u> Dru.	<u>satellititia posticatus</u> Grt.			<u>satellititia posticatus</u> Grt.	<u>MADORYX</u> <u>bubastus butleri</u> Kirby
<u>vitis hesperidum</u> Kby.	<u>v. vitis</u> (as on continent)	<u>v. vitis</u> Linné	<u>v. vitis</u> Linné	<u>vitis fuscatus</u> R. & J.	<u>SESTIA</u> <u>tantalus clavipes</u> R. & J.
<u>XYLOPHANES</u> <u>c. chiron</u> Dru.	<u>chiron cubanus</u> R. & J.	<u>**chiron nechus</u> Cram.	<u>**chiron nechus</u> Cram.	<u>chiron lucianus</u> R. & J.	<u>AMPELOECA</u> <u>myron mexicana</u> Gehlen
					<u>ARCTONOTUS</u> <u>terlooi mooseri</u> Clark
					<u>XYLOPHANES</u> <u>amadis cyrene</u> Druce <u>thylia salvini</u> Druce

* These are not 2 subspecies from the same locality but are from different islands.

**Both Draudt and Forbes have this subspecies occurring in Puerto Rico and Hispaniola; I would expect that X. chiron might occur, but not the continental nechus. I have seen no specimen from these two islands myself.

SUBSPECIATION SYMPOSIUM. Cary: West Indian Sphingidae- concl.

it has become subspecies insularis, with the median light spots on the costal and lower margin of the forewing merging to make a solid light median band on this wing. P. insularis is said to occur on Hispaniola but I have seen no specimens from there. P. syces cubensis is very much smaller, monotonously dull brown with only the light apices and costal spots distinct. I have syces from Santa Catarina, Brazil, in which the light spots are close together, almost joining as in insularis, and there is a specimen reported from Mexico where this is also true.

In Pholus satellitia we again have the nominotypical subspecies in the West Indies (Jamaica). This is another species so variable that were it not for its constantly double cell-spots, we would hardly recognize some of the forms as belonging to this species. We think at once of the common P. satellitia pandorus (Hbn.) of the eastern seaboard of the U.S.A. and of the very common P. satellitia lichaon (Cram.) of South America and Trinidad. Cuba has the beautiful subspecies posticatus, found also on the Bahamas. A color form of posticatus occurring in Cuba is called cinnamomea, often recorded as a subspecies of satellitia. The well known and beautiful Pholus vitis vitis of Florida, Mexico, South America, and Trinidad is found on most of the Greater Antilles (Cuba, Hispaniola, Puerto Rico) but on Jamaica is found the much darker and handsomer race hesperidum, whose underside is red and whose forewing has two instead of three horizontal curving white lines. P. vitis fuscatus is found on the Lesser Antilles, in general a less clearly marked and more suffused subspecies. In Xylophanes chiron we have another nominotypical subspecies in Jamaica, with X. c. cubanus in Cuba, and X. c. luciana on the Lesser Antilles. The very common Xylophanes chiron nechus is the continental form found in Florida, Mexico, Venezuela, etc. In one night at light in Venezuela we took 110 specimens of nechus!

For easier comparison I have added a table to show the endemic subspecies of Sphingidae on the Antilles, a much greater number than in Florida or a comparable area of continental South America, especially nearby Venezuela. Florida has three endemic subspecies (Dolba hylaeus floridensis Clark, Ampeleoca myron chotus Hbn., Amphion nessus floridensis Clark); Venezuela has two (Isognathus rimosa papayae Bdv. and Xylophanes germen yurakano Lichy). Trinidad also has papayae and the endemic race, trinitas Closs, of Xylophanes neoptolemus. Mexico, however, because of its differences in environments, its deserts, high tablelands, and towering snowpeaks, its jungles and other natural barriers, has twenty-three endemic subspecies of Sphingidae. I have listed them all on the table; but one, Nannoparce poeyi haeterius, is of special interest from the point of view of geologic history. N. p. poeyi, the nominotypical race, is found in Jamaica, Cuba, and Hispaniola, and for this species we find a subspecies in Yucatan. There are geologists who believe there was a former land connection between Yucatan and the western end of Cuba. This is also suggested by Xylophanes porcus, recorded in the West Indies only from Cuba and widely represented in Mexico, Venezuela, etc., by X. porcus continentalis R.&J. Unfortun-

nately the rocks have so far revealed no sphingid fossils so we must guess at the geological history of our Antillean Sphingidae. Hurricanes and some form of water transportation probably account for the wafting of these moths to the Islands, perhaps in the Miocene after the re-emergence, and there are probably continuing invasions of some of the stronger flying Sphinx-moths either by direct flight over water or carried via ships.

There seems to me to be little in favor of the idea that the differences between the island subspecies of Sphingidae on the Antilles are of adaptive significance in evolution. All of the Antilles are much alike in their climate, foodplants, etc., yet the populations of Sphingidae on the different islands, relatively only a few miles apart, have developed into differentiated subspecies. We have no wide deserts or high mountains to act as barriers.

There is considerable evidence suggesting different invasions of Sphingidae on the West Indies. In the case of Erinnyis obscura jamaicensis there is evidence of an ancient invasion and geographic isolation causing this species to evolve into a subspecies. Erinnyis o. obscura is also caught in Jamaica, and this points to a second, much later invasion, where the two forms met but remained segregated because of developed gene discontinuities. Another sphingid moth showing evidence of different invasions is Phlegethontius rusticus, already referred to. It looks as though P. rusticus cubanus and P. r. dominicanus had become distinct before the secondary invasion of P. r. rusticus to these islands.

Whether the West Indies are in fact purely oceanic islands or are fragments of a continent, the Sphingidae have developed as though they were oceanic islands. Mayr writes, page 173: "Oceanic islands are defined as all those islands that have received their fauna from other islands or from neighboring continents by transoceanic colonization, and not over land bridges." Sphinx moths evolved late among Lepidoptera. Their distribution on the Antilles is, I believe, largely transoceanic. Still, there were certain connections geologically among the islands of the Greater Antilles that are of special interest in viewing subspeciation of Sphingidae. At one time Jamaica was undoubtedly connected with Hispaniola. At another time Hispaniola was connected with Cuba. The distribution of Sphingidae on Hispaniola, so far as our insufficient data go, indicates a clear relationship to both Cuba and Jamaica. The distinctness of island populations of Sphingidae in the Antilles seems to depend on the size of the island, the length of geologic time in its effective isolation, and the amount of chance dispersal over water and through the air. These factors coupled with the small size and isolation of populations, with certain species which because of localized foodplants tend to become sedentary and restricted in range, with some cases of repeated invasions, and with certain moths more given than others to variation, seem adequate causes to produce the 32 existing subspecies of Sphingidae in the West Indies.



III. HOLARCTIC BUTTERFLY SPECIATION AND SUBSPECIATION, ESPECIALLY IN NORTH AMERICA

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The term "Holarctic" is used to refer to the biota of the boreal regions of both the Old and New Worlds; "Palaeartic" applies to the subdivision in the Old World, and "Nearctic" to that of the New World. Be it noted that in this article these terms are used with specific reference to ORIGINS, and not necessarily to distributions. Many organisms now occurring widely in the boreal regions had their origins elsewhere. In any attempt to study their history we must consider such forms with the biota as a part of which they evolved, and not with one into which they may have subsequently migrated.

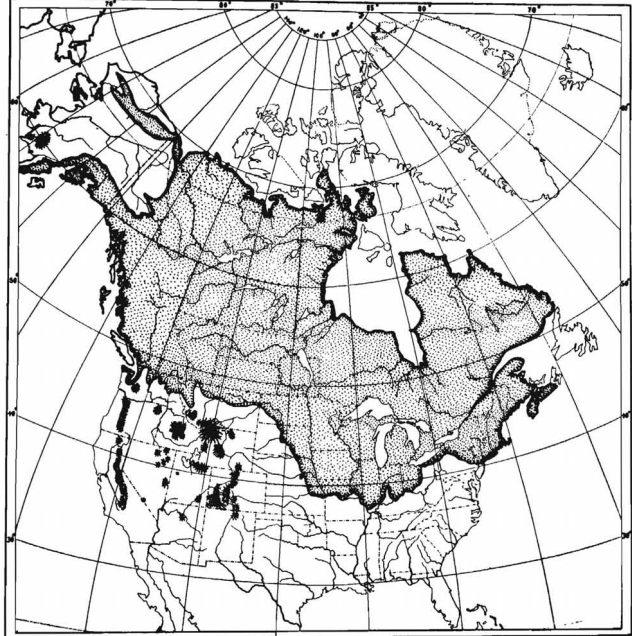
Thus, a great many of the North American butterflies are Neotropical in origin. Some familiar examples are: SATYRIDAE - *Euptychia*; all HELICONIIDAE; NYMPHALIDAE - *Euptoista*, *Anartia*, *Eunica*, *Anaea*; most or all RIODINIDAE; LYCAENIDAE - *Eumaeus*, *Atides*, many species of *Strymon*, *Leptotes*, *Hemiarctus*, etc.; PAPILIONIDAE - *P. philenor* L., *polydamus* L., *marcellus* Cram., etc.; PIERIDAE - *Anteos*, *Phoebis*, *Kricogonia*, *Eurema*, *Appias*, and *Ascia*; HESPERIIDAE - *Phocides*, *Polygonus*, *Epargyreus*, *Heliopetes*, *Atrytone*, *Atrytonopsis*, *Lerodea*, *Calpodes*, *Panoquina*, etc. We must exclude all such from a study of the purely Holarctic fauna.

Again, some of our North American butterfly groups are probably autochthonous, i.e. originated here. Lacking the evidence of palaeontology we are greatly handicapped in considering this. We must remember how fossil records, reversing earlier belief, showed the horses to have been of North American origin; and the camels to have originated in South America whence they spread, via North America (where they subsequently died out) to the Palaeartic. Most likely of our butterflies to be autochthonous are the *Papilio* of the *glaucus* and *troilus* groups; all *Speyeria*; and, perhaps, *Zerene*, *Incisalis*, *Erora*, and the *Tharsalea* subgenus of *Lycaena*.

Studies of evolution have shown that no population can evolve into a biologically separate species unless it is effectively isolated from any other population with which it could interbreed. Such isolation, be it noted, is a prerequisite but not a cause of evolutionary differentiation. Any study of Palaeartic vs. Nearctic speciation and subspeciation must, therefore, be primarily concerned both with the factors that have isolated Old and New World populations from each other, and also with those which have isolated populations from each other within the regions.

The greatest of these isolating factors was the series of southward extensions of the northern ice cap during the last geologic epoch, the Pleistocene (see Map). At least four such glaciations are known to have occurred, alternating with periods of glacial recession when a relatively uniform, perhaps even subtropical climate prevailed over most of the globe. In North America the earliest of the glacial periods is known as the Nebraskan; the second, the Kansan; the third, the Illinoian; and the

most recent, the Wisconsin. More or less corresponding periods have been identified in Europe and, to some degree in northern Asia.



CONTINENTAL PLEISTOCENE GLACIATION OF NORTH AMERICA
Greenland and the other islands were also largely ice-covered. Shore-lines varied greatly due to changes of the sea level. Note the large unglaciated area of Alaska, the Yukon, and probably Siberia.

The ice must have pushed most or all butterflies ahead of it as it moved southward. A very large part of Alaska, from the Bering Sea to the upper Yukon was never, however, ice-covered. Perhaps some species survived here. Certainly many of the most northern species must have managed to survive very close to the edge of the ice sheet, as we see their descendants doing in Greenland today. But their ranges certainly extended far to the south of the southern limit of the ice; and less northern species of course extended still farther southward. Moreover, considerable areas of local glaciation developed in the Rocky Mountain and Sierran systems south of the main ice sheet. These two systems (and to a lesser degree the Appalachian chain) then formed three elevated highways along which the northern species were able to extend farther southward than in the intervening lower areas. The north-south mountain chains also, be it noted, formed barriers across which east-west dispersal of less cold-adapted species could not take place. This is in striking contrast to the effect of the mountains of Europe and Asia, which run roughly across the line of advance of the ice rather than parallel to it.

Then, as the ice sheet receded northward, the biota must have followed very closely. As the cli-

SUBSPECIATION SYMPOSIUM. Klots: Holarctic Butterfly Speciation- cont.

mate became warmer the more cold-adapted species were forced out from the lower and more southward regions first, progressively up the slopes of the mountains as well as northward. On the highest mountains, where the climate still approximates that of the far north, some of even the most Arctic species have managed to survive even to the present time. These are the well known "relict forms". It followed that these mountain populations of far-northern species became, in time, isolated from the northern populations. In many cases, moreover, the mountain populations themselves have become broken up into isolated groups, since the mountain chains are cut across by areas of lowland sizable enough to constitute barriers impassable by the mountain forms. Thus was formed, and still exists, the isolation necessary for the mountain populations to evolve specific or subspecific divergence, not only from their northern "cousins" but also, to some degree, from each other.

A clear understanding of the population isolations resulting from the glaciations is essential to any study of distribution speciation and subspeciation. To this must be added a host of other isolating factors ranging from the east-west variation in humidity, north-south variations in temperature, and local environmental (ecotopic) effects.

Today each of the mountain systems has some of the relict forms. The Rocky Mountain chain, the most extensive and continuous, is by far the richest. The Sierran, with much less extensive Arctic-Alpine areas, and broken by a wide gap between Washington and California, has fewer. The Appalachian, much older and more eroded, has only three areas where true Alpine Zone occurs. These are: the Shickshock Mts. in the Gaspé; Mr. Katahdin in Maine; and the Presidential Range in New Hampshire. The Appalachian has the smallest Arctic-Alpine butterfly fauna of the three.

It will be noted that at least four glacial periods are known. Exact details of the extent of the ice in each are not fully known, especially for the earlier periods; but probably these did not differ in any major way (from the viewpoint of the biologist, at least) from that of the most recent, the Wisconsin. Each of these periods with its following interglacial period was certainly responsible for isolating many butterfly populations. Very possibly some of the more distant degrees of relationship that we can trace today date from one or another of the earlier isolations.

Before considering in detail any butterfly speciation and subspeciation, we should note one other pertinent point. Populations of some of the essentially far northern groups of the Holarctic butterflies have, by adapting to life in a somewhat milder climate, succeeded in surviving and even in extending their ranges far southward at low elevations. Notable among these are species which survive as relicts in the true acid bogs of southern Canada and the northern United States. Since the flora of these bogs is exceedingly like that of the far north, a great many plants being common to both,

adaptation by the butterflies has chiefly consisted of evolving the ability to survive during a longer warm season at higher temperatures, and has not involved food plant changes. We thus find such butterfly species as Boloria freija and eunomia ("aphirape"), Geneis jutta Hbn., and Lycaena epixanthe Bdv. and Lec., specific or subspecific offshoots of essentially northern populations, existing well to the southward in isolated populations in bogs.

Limitation of space permits mention here of only a few examples of the various degrees of speciation and subspeciation of Holarctic butterflies that have occurred in North America. Ignorance is also a powerful deterrent; for relatively little attention has been paid to this matter.

Zerene, whether regarded as a subgenus of Colias or as a separate genus, evidently arose from the sex-patched group of Colias, from which it has become greatly differentiated. It has extended its range to southern South America. Perhaps it, as well as the Colias (Scalidoneura) species limited to South America, first became isolated during a pre-Wisconsin glacial-interglacial period. Contrasted with Zerene, Colias meadii Edw. has developed, at most, specific distinction from its Palaearctic sex-patched relatives. Its two more or less isolated populations (the southern meadii and the northern elis Stkr.) are now evolving subspecific distinction from each other. Perhaps meadii first developed specific distinction following the Illinoian glaciation, and its present subspeciation in post-Wisconsin. Similarly Colias behrii Edw. and harfordii Hy. Edw. of California may represent species dating from pre-Wisconsin isolations, the first having evolved from Colias nastes stock, the second from the C. chrysotheme complex. And the C. eurytheme-philodice populations, likewise descended from the chrysotheme complex, and at present vacillating in an indescribable (and insufficiently known) state of partially specific, partially subspecific separation from each other, appear to be specifically distinct from harfordii and presumably likewise from the Palaearctic chrysotheme Esp.

Among our other Colias, the Willow-feeding C. gigantea-harroweri-scuttelleri-ruckesi populations appear to have evolved as a distinct specific stock with fairly well differentiated subspecies, extending from the Arctic to New Mexico. The Legume-feeding C. alexandra-edwardsii-emilia-christina-krauthii population is certainly specifically distinct; but its two main components, traditionally called alexandra Edw. and christina Edw., are hardly specifically distinct from each other although some definite subspecific distinctions can be traced within them.

The distinctive Colias nastes Bdv. has evolved some more or less clinal subspecific distinctions in North America, but is probably not specifically distinct from Palaearctic populations. The same is true of C. hecla Lefebre and, perhaps, of C. palaeno L. In these species the lack of specific distinctions between Palaearctic and Nearctic populations must be due to a longer period of interbreeding

between the Palaearctic and Nearctic, a process facilitated by their Arctic habitat.

Colias is evidently undergoing some very puzzling changes today. This is commonly attributed to a present rapid rate of differentiation. An alternative hypothesis must, however, receive serious consideration. Perhaps the pre- as well as post-Wisconsin isolation of some of the species was less complete (due to strong flight habits?) or mutational changes during the isolations were less effective, or both. As a result, various populations of the ancestral stocks of the eurytheme-philodice and alexandra-christina complexes split into subpopulations less completely genetically differentiated from each other. And so we see today the results of varying rates of interbreeding as these incompletely differentiated populations come together again. The same situation occurs on a smaller scale in the Limenitis arthemis-astyanax population.

Turning to Boloria, a genus similar to Colias in possessing rich representation in both the Palaearctic and the Nearctic, and also in both far northern and temperate environments, we see a more stabilized pattern. There is, in North America at least, little evidence of such hybridization as we see in Colias. Therefore, we may infer that pre- and post-Wisconsin isolations were more complete. Boloria shows, however, some widely varying degrees of speciation and subspeciation.

Both B. freija Thunb. and B. polaris Bvd. show relatively little differentiation of the Old and New World populations. The range of freija in North America is great, extending all across the Arctic and south in the mountains into Colorado and in bogs into Quebec. Despite this, little subspeciation is evident. The far northern population is distinguishable as the large and dark tarquinius Curtis; and perhaps both natazhati Gibson and nabokovi Stallings and Turner from the northern Canadian-Alaskan mountains represent a similar local subspeciation. Elsewhere no distinct subspecies of freija are discernible.

Boloria titania Esp., eunomia Esp., and selene L. are even more widely distributed in both the Palaearctic and the Nearctic; but in contrast to polaris and freija these species have broken into a great number of subspecies. B. chariclea Schneider of the true Arctic may or may not be considered conspecific with titania, depending on one's tendency to "lump" or "split". But in any case we can clearly place in titania the Nearctic subspecies boisduvalii Dup., grandis B. and McD., rainieri B. and McD., ingens B. and McD., helena Edw., and montina Scud. In eunomia we may place denali Klots, tricoloris Hbn., dawsoni B. and McD., laddi Klots, and caelestis Hemming. In selene we may place alboquina Holl., atrocotalis Huard, tollandensis B. and Benj., terra-novae Holl., nebraskensis Holl., myrina Cram. and marilandica A. H. Clark. Of all our species of Boloria, selene has been most able to adapt to more southern conditions, which explains its wide range and has permitted its great subspeciation.

In the frigga group of Boloria some rather more fundamental splits have occurred. In the Nearctic occur four distinct species, of which at least two (and perhaps all four) are endemic. B. frigga Thunb. and B. improba Butler occur in both Old and New Worlds but have, as far as we know (northern Asiatic material is lacking) greater range and differentiation in the Nearctic. B. frigga has at least two northern subspecies, gibsoni B. and Benj. and saga Staud., and a third, sagata B. and Benj. in Colorado. B. improba, a truly Arctic butterfly, has a slightly sub-Arctic subspecies youngi Holl. in North America, as well as the Palaearctic improbula Bryk. B. epithore Edw. is clearly endemic (British Columbia and Montana to California and Colorado). And B. toddi Holl. (= bellona Fab.) ranging from western Canada to New Jersey has, like selene, adapted to a wide climatic range; but unlike selene it shows little distinctive subspeciation. Only two named subspecies are recognizable, ammiralis Hemming and jenistae Stallings and Turner; and the latter is really more of a local form than a major subspecies. Very possibly the four species all attained specific distinction in pre-Wisconsin times.

Only a few of the Holarctic butterflies have been touched upon above. Perhaps, since space forbids more detailed treatment, a listing of some of the other more prominent examples will be of interest, roughly classified as to the degree of differentiation that has evolved between the Palaearctic and the Nearctic populations. The majority of these are, of course, the lowland and warmer climate forms which, I fear, have been most unjustly skimmed above.

SPECIFIC DIFFERENTIATION: Papilio polyxenes Fab., brevicauda Saunders, zelicaon Luc., etc.; Parnassius; Anthocaris and Euclœ; Pieris virginiensis Edw., protodice Bdv. and Lec., beckeri Edw., etc.; Coenonympha haydeni Edw.; Cercyonis; Oeneis and Erebia, many species; Euphydryas, Melitaea, and Polygonia; Nymphalis californica Bdv., milbertii Latr., and j-album Bdv. and Lec.; Vanessa virginensis Drn.; Limenitis; some Strymon; some Lycaeides (e.g. melissa Edw.); some Plebeius (e.g. saepiolus Bdv.); some Pyrgus (e.g. communis Grote); many Hesperia.

SUBSPECIFIC DIFFERENTIATION: Papilio machaon L.; Pieris napi L.; Coenonympha tullia Muller; Oeneis taygete Gey., jutta Hbn., norna, and melissa Fab.; Erebia theano Tausch.; Lycaena phlaeas L.; Lycaeides argyrognomon Bergstr.; Plebeius aquilo Bdv.; Lycaenopsis argiolus L.; Pyrgus freija Warren; Carterocephalus palaemon Pall.; Hesperia comma L.

AT MOST VERY MINOR SUBSPECIFIC DIFFERENTIATION: Nymphalis antiopa L.; Vanessa atalanta L. and cardui L.

As previously mentioned, the route between Alaska and northeast Asia seems to be the only one by which any significant movements of butterfly populations between the Palaearctic and the Nearctic have taken place. There is but little evidence, and that dubious, of any effective direct migrations between Europe and eastern North America. The butterflies of

SUBSPECIATION SYMPOSIUM. Klots: Holarctic Butterfly Speciation- concl.

northwestern North America show, in general, closest relationship to those of northeastern Asia; and the further we trace, south and east in North America and south and west in Eurasia, the greater become the differences from the meeting point.

In making such comparisons one must, of course, be watchful for the possibility, or even probability, of parallel evolution having occurred in both Old and New Worlds, as species became adapted to similar environments in central Eurasia and central North America. A number of such cases of parallelism seem to be discernible. One striking instance is evidenced by the great similarity of *Boloria t. titania* and *B. t. grandis*; another by the resemblance of *Lycaena p. phlaeas* to *L. p. americana* Harris; and still another by the great similarity in Europe and North America of the more southward subspecies of *Vanessa atalanta* and *cardui* and *Nymphalis antiopa*. Many more such possibilities could be cited.

Detailed studies comparing the Palaearctic and Nearctic butterflies are largely lacking. Such as

exist are weakened by our still great ignorance of the Nearctic forms. First we must have studies of these on a far more exhaustive and detailed scale than have been made. We do not yet know even the major subspecific patterns of the majority of our species. There must be far more thorough collecting, and large collections must be gotten together and be made available, on a scale hitherto unknown, to the taxonomic specialist. And the specialist himself must change his ways and, instead of trying to cover all groups in a broad geographic field, must concentrate his efforts on complete coverage of smaller taxonomic groups.

If this is done, there is some hope that in a few generations we may come to know the Nearctic butterflies as well as those of Europe are now known. Of course, the vital annectant area of Asia will very likely continue essentially unknown for much longer. Eventually, let us hope, studies like the present one (which is really but a superficial survey "conceived in ignorance and begotten in haste") may come to have real significance.

IV. SUBSPECIATION IN EUROPEAN LEPIDOPTERA

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In a paper of this length it is possible to discuss only briefly and in very general terms a few of the many aspects of subspeciation in the European Lepidoptera. In Europe, most subspecies have developed in populations that were isolated from other populations of the same species by the great climatic and vegetational changes that took place during and since the Ice Age. Conditions appear to have been more conducive to the isolation of such populations in Europe than in North America. The primary reason for this is that in Europe the chief mountain ranges - the Alps and the Pyrenees - run east and west. They, and the ice sheets that developed on them, formed a barrier that prevented populations of some species from retreating southward from north-central Europe as the main ice sheets advanced from the north and as the climate deteriorated. These populations, being cut off from the main populations of the same species that survived in Europe south of the glaciated areas, were able to develop independently. In North America the chief mountain ranges run north and south, so that the Lepidoptera were able to retreat southward along or between them as the ice sheets advanced from the north, and, in general, populations were not cut off to the same extent as in Europe. Because of the directions of the mountain ranges, too, the number of purely mountain species as compared with purely northern or northern and mountain species is probably smaller in North America than in Europe.

During a glacial phase, Europe south of the main ice sheets and north of the Alps and the Pyrenees

was inhabited by two main groups of species: first, species that had inhabited the northern regions and the mountains during the preceding temperate phase and that had been driven by the expanding ice sheets from those areas into north-central Europe; and, second, species of which populations had inhabited central Europe during the preceding temperate phase and had been cut off from the main populations by the development of the mountain ice sheets.

In the species of the first group, subspecific variation has developed mainly since the chief ice sheets retreated. As they are species characteristic of cold climates, the climatic amelioration as the ice retreated was the main factor in dividing the range of each into small populations that could develop independently of each other. Some retreated into the mountains, where many of them became divided into small populations, each on a different mountain or group of mountains. The independent development of such populations is particularly striking in *Erebia*. *Erebia tyndarus* Esp., for example, has had some 15 described subspecies in the mountains of central Europe. Other species retreated into northern Europe. On the whole, these did not develop subspecies to the same degree as in the mountains. The main reason for this is that habitats ecologically suitable to them extend more or less continuously over large areas in the north, so that the species' ranges are not divided up into isolated populations as in the mountains. Some species retreated both into the mountains and into northern Europe. These are the species that now have the

so-called boreo-alpine or arctic-alpine types of distribution. Some of them developed subspecies independently in both regions. Erebia medusa Schiff. and Dennis, for example, is represented by one subspecies in northern Europe and by at least nine others in the mountains of central Europe.

The populations of species characteristic of temperate climates that were cut off from the main populations of the same species in north-central Europe during glacial phases developed independently during their periods of isolation. As the ice sheets advanced and the climate deteriorated, they were faced with three possibilities: they might die out completely in north-central Europe; they might adapt themselves for life under the new conditions; or they might become confined to those parts of the ice-free area where ecological conditions favorable to them still existed. Most populations probably were forced to take the first course; naturally, the identities of such species concerned unknown.

There is evidence that some populations changed their habits to survive. A number of species are each represented by two races in Europe, one having a wide and more or less continuous distribution, inhabiting woodlands or grasslands, and feeding on woodland or grassland plants, and the other having a boreo-alpine type of distribution and occurring also in the northern and western parts of the British Isles, inhabiting heaths and moorlands, and feeding on heath and moorland plants. In each case, the latter probably represents a population of the species that was cut off in north-central Europe during a glacial phase, became adapted for life in the cold climates and among the heath and moorland vegetation that must have covered much of that region, and then retreated to the areas where such conditions existed when the ice sheets retreated and the climate became warmer. While they were retreating northwards and into the mountains, the other races of the same species that had survived in Europe south of the glaciated areas with unchanged habits spread over central Europe. At present the distributions of the two races of the one species often meet or overlap; but in most instances apparently little or no interbreeding occurs, as they are isolated from each other by the habitat differences. In some instances, they are also isolated by differences in the times of appearance of the adults, as in Hydriomena furcata Thunb., whose moorland race appears about a month before the woodland race. Some of the moorland races differ morphologically from other races of the same species and on morphological grounds are regarded as good subspecies; others differ but slightly and not constantly. In the preceding, the term "race" is used for convenience. It would be perhaps more correct to consider the moorland races as distinct species, at least in some instances.

Most of the populations that survived a glacial phase in north-central Europe did so by becoming confined to those areas where ecological conditions favorable to them still existed. The chief area of refuge for many of the species appears to have been land between the present south coasts of the British Isles and the north coast of France. This area was land at that time because of the lowering of the

sea level that took place during glacial phases as a result of the locking-up of great quantities of water in the ice sheets. The climate there was less cold than elsewhere because of the proximity of the ocean, as well as because of the distance of that region from the ice sheets and its low altitude. While they were isolated there or in adjacent ice-free regions, populations of many species developed subspecific characters. When the ice retreated and the climate gradually became warmer, these populations spread out from their areas of refuge. At the same time, other populations of the same species, which had survived in Europe south of the glaciated areas, spread northwards and westwards. Eventually the ranges of the two subspecies of each species met. Interbreeding then took place as, unlike the moorland races described above, in most instances the two were not isolated from each other ecologically. The invaders from the south usually overwhelmed the descendants of the relict populations, and the latter now survive only in geographically isolated regions into which the former were unable to spread in any numbers. In some instances, the invaders from the south did not reach western Europe until after the British Isles had become separated from the European mainland by the sea. These species are now represented throughout the British Isles by descendants of the relict populations. Bena prasinana subsp. britannica Warren is an example. In other instances the new invaders reached Great Britain but not Ireland or the islands of Scotland, so that the species are represented by descendants of the relict population in the latter areas but not in Great Britain. The satyrid butterfly, Maniola jurtina L., is an example, its relict population being represented by the Irish subspecies lernes Graves, the Hebridean subspecies splendida B.-White, and Scilly Isles subspecies cassiteridum Graves. That the two subspecies of the one species are interbreeding where their ranges meet on the one land is shown by the relatively narrow zone of intergrading between the two in such cases. For example, intermediates between Aricia agestis subsp. agestis Schiff. and artaxerxes Fab. are found where the ranges of the two Blues meet in parts of western Scotland.

Apparently some relict populations were forced to become inhabitants of the sea coasts to survive a glacial phase in the region of the British Isles, and have retained their maritime habits to the present day. Other populations of the same species, besides usually differing morphologically, inhabit inland localities on the European mainland, many of them being characteristically mountain species. Hadena andalusica Staud. is an example. However, as there is at present no known definite instance where the ranges of the two populations of such species meet or overlap, it is not possible to state whether or not they are ecologically and reproductively isolated from each other, and therefore whether or not they should be regarded as subspecies or as distinct species. It is possible that cases parallel to these may occur on the coasts of North America. Investigation of this is desirable as it might throw more light on the origin and status of such subspecies.

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V. SUBSPECIATION IN THE MICROLEPIDOPTERA

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It is well known that in such groups of animals as birds, mammals, and butterflies the patterns of speciation are largely geographic, and that we can demonstrate every transition from minor geographic differentiation within a single species to the broadest cleavage between geographically representative species or even species groups. Such authors as Rothschild and Jordan (1903) and Mayr (1942) have emphasized the significance of geographic speciation, and there is no doubt that this process has been of dominating importance in the evolution of the higher Lepidoptera. My own work on West Indian butterflies has, for example, led me to adopt hypotheses that closely resemble those Mayr has advanced to explain the distributions of South Pacific birds.

In such groups of microlepidoptera as the Pyralidae, similar patterns are easily discovered. Contrasting the European with the American fauna, we see in some cases a simple subspecies difference, as in *Crambus hortuellus* (Hbn.) or *Pyrausta funebris* (Strom.). In other instances there is a species difference, as between *Crambus dumetellus* (Hbn.) and *U. rubigalis* Gn. In still more extreme cases a species group in Europe appears to represent a species group of North America, for instance, the *Pyrausta aurata* (D. and S.)-*purpuralis* (L.) group of Europe as opposed to the *P. ochosalis* *Dyar-generosa* (G. and R.)-*tuolumnalis* B. and McD. group of America. On the other hand, some species of Pyralidae do not differ appreciably from North America to Europe. Examples of this kind increase in numbers in higher northerly latitudes; we may cite *Scoparia centuriella* (D. and S.) or *Udea inuinatalis* (Zell.).

Subspeciation may of course also occur in a much smaller field. Thus *Pyrausta unifascialis* (Pack.) has three subspecies, one in northeastern, one in northwestern, and one in southwestern North America. *Pyrausta perrubralis* (Pack.) also has three subspecies, one east of the Rockies, one in California, and one on Vancouver Island. Northern as against southern subspecies also commonly occur, and the dividing line may be situated at different latitudes: in *Crambus albellus* Clem. near the Canadian-U.S.A. border, in *Phlyctaenia extricalis* (Gn.) in the middle states, and in *Polygrammodes flavidalis* (Gn.) in Florida. Other, less typical, patterns are found in *Pyrausta napaealis* (Hlst.), which appears to have one subspecies on the coast of California and another in the interior, and in *Loxostege albicerialis* (Grt.), which has one subspecies in the western United States and another in Florida.

Geographically representative pairs of species can also be found in North America, e.g., *Onidea lunulalis* Hlst. in the eastern part of the continent, and *O. luniferella* in the west. Even more interesting are pairs or sets of species the distributions of which suggest that they have until

very recently been geographically representative. *Mecyna submedialis* (Grt.) ranges from eastern Canada westward to the Rockies; on the Prairies its range overlaps that of the closely allied *M. mustelinalis* (Pack.), which, in turn, extends southward to southern California and Arizona, where it is sympatric with a third member of the complex, *M. luscitialis* (B. and McD.). This combination of ranges strongly suggests that the three species were originally geographically vicarious, and that they have subsequently become partially sympatric through local extensions of range. Another interesting case is that of the pair *Pyrausta ochosalis* Holl. and *P. tuolumnalis* B. and McD. The first-named species ranges east and west across Canada from coast to coast; the range of the second lies along the Cordillera, from California to the Yukon and Northwest Territories, transecting the range of *P. ochosalis* at right angles.

Thus, in the Pyralidae, as in the macrolepidoptera, we see every stage in the cycle of geographic subspeciation and speciation widely exemplified. Had we sufficient knowledge of tropical insular faunas, there is no doubt that we could assemble far more impressive and convincing series than we can do in the relatively unfavourable environment of the temperate continents. There is certainly little doubt that geographic speciation has been of considerable importance in the evolution of the Pyralidae.

Now, it is worth noting that the Pyralidae stand, both phylogenetically and biologically, at a level intermediate between that of the macrolepidoptera and that of the true microlepidoptera. It is possible that they occupy a similar position in the field of speciation mechanics.

The examination of a large collection of North American microlepidoptera shows one thing very strikingly. This is that, except in the Pyralidae, and in a few families such as Cossidae and Hepialidae that include individuals of large size, geographic variation within species is, at least so far as can be determined by gross examination, almost negligible; this appears to be true also in important groups of the Pyralidae.

I am able to give a few examples of geographic variation in microlepidoptera *argentialbana* Wlsh., from the Prairies, with its larger and more heavily maculated subspecies *britana* McD. in British Columbia; *Epinotia hopkinsana* Kft., from British Columbia, with its subspecies *cupressi* Heinr. from California. A somewhat different case is that of the well-known *Archips persicana*, which in western North America has what appears to be a dimorphic form, in which the costal spot, normally triangular and contrastingly white, is reduced to a narrow, almost concolorous quadrangle. I repeat, however, that these few examples have been selected, after considerable search, from among a great mass of species that show no evident geographic variation.

Not only do most species of microlepidoptera lack obvious geographical variation, but they also have another interesting group characteristic: they are in a very large part monophagous or narrowly oligophagous. This introduces a further generalization: whereas in many groups of animals very closely related species tend to be allopatric, in the microlepidoptera this does not seem to be the case, but instead closely related species tend to be sympatric, being distinguished primarily by different host plant preferences. We do not have enough definite information for the assembly of statistics, but certainly the host-plant species pattern is dominant in a wide range of groups, of which I may mention as examples Acrobasis, Coleophora, Lithocolletis, Nepticula, and the Aegeriidae, among many others.

Examining this tendency in detail, we find that some specific examples have been well investigated. The work of Thorpe (1929) showed the existence of at least two morphologically similar, but biologically distinct, forms of the European Hyponomeuta padella L. These differ in food plant requirements, and behave in mating and oviposition as discrete populations. Although Thorpe, impressed by the morphological similarity of the apple-feeding and hawthorn-feeding populations, classed them as "biological races" of the single species H. padella, the evidence that he presents leaves no doubt that they are in reality distinct species in the Dobzhansian or functional sense. Somewhat more subtle problems are suggested by Thorpe's remarks on some of the other members of the H. padella complex.

A more difficult situation certainly exists in the budworms of the genus Choristoneura. As Freeman (1947) has noted, there are in eastern Canada two species of this genus which are barely distinguishable on morphological characters, but which differ sharply in seasonal periodicity and also in their food plants, one being the notorious spruce budworm, the other being a pest of jack-pine. So far the situation does not differ greatly from that found by Thorpe in Hyponomeuta. In British Columbia, however, there exists a population that appears to be intermediate in morphological characters between the spruce and jack-pine budworms of the east; this intermediate population has been reported from spruce, pine, and Douglas fir.

Even finer degrees of difference have been investigated in the codling moth, Carpocapsa pomonella (L.). It is well known that in California, southern Europe, and elsewhere, the codling moth attacks not only apples and other fruits, but also walnuts. In California, this habit is believed to have been adopted by the species at a time subsequent to the establishment of the insect there as a pest of apples. Accordingly the possibility has been investigated that two genetically distinct and perhaps reproductively isolated populations of the codling moth exist in California. The results of such investigations have up to the present time been equivocal or negative (Boyce, 1935; Smith, 1941, Basinger and Smith, 1946). A more interesting case was, however, reported by Armstrong (1946). This - the apparently local origin of a univoltine

strain of C. pomonella in an isolated pear orchard - illustrates very well how microgeographic differentiation, aided by a tendency to host specificity, may play a part in the evolution of microlepidoptera.

In the microlepidoptera, then, we have a reversal of the geographic speciation pattern that is so evident in such groups as the macrolepidoptera, the mammals, or the birds. With our present knowledge we cannot say that the different pattern is the result of a different mechanism of speciation; but this possibility certainly ought to be investigated. To try to anticipate the results of such an investigation would be premature, and I have no wish to do so. I should like, however, to mention one or two points that may have a bearing on the matter.

This pattern of sibling species, apparently isolated by host preferences, is by no means confined to the microlepidoptera, but on the contrary appears in a wide variety of groups, among which I may mention the Chrysomelidae and other phytophagous Coleoptera, and the various phyla of parasitic helminths. The thing that all these groups have in common is that many of their species exhibit a narrow and rigid host specificity, which is only under exceptional circumstances broken down. Experimental studies have shown that transfer from a normal to an abnormal host is usually accomplished only in the face of a serious selective disadvantage; the typical course of events is for a high initial mortality to be followed by the establishment of progeny of the few survivors, as a strain adapted to the new conditions. No doubt adaptive change might proceed rapidly in the new and strange environment, and within a few generations it might become hard to make the transition back to the original host. If the odds against establishment on a new host are fairly high, this provides the basis for a mechanism that would isolate from the parent stock any strain that does succeed in making the change.

Another theoretically possible basis for the sympatric development of host-specific strains is provided by the "host-selection principle" of Hopkins (1916); and also Craighead (1921). The principle postulates that the species chosen by a female insect as a host for oviposition is in some cases determined by the identity of the host on which that female fed in the early part of her life. The extent and regularity of the application of this principle have yet to be investigated. If its validity should be established, however, Hopkins' principle would constitute a second potential isolating mechanism between strains of a species on different host plants.

Yet a third possibility is that of a sort of micro-geographic differentiation, such as was suspected by Armstrong in the case of the pear-orchard strain of the codling moth, mentioned above. Some combination of these processes, perhaps with the addition of others whose existence is not yet suspected, may suffice to explain the speciation patterns of the microlepidoptera and similar groups.

Certainly, whatever the eventual conclusion may be, the possibility of speciation governed primarily by host-plant isolation deserves attention. Nor

SUBSPECIATION SYMPOSIUM. Munroe: Microlepidoptera- concl.

should the evolutionary patterns of the microlepidoptera be studied as though they were the anomalies of some obscure and insignificant group: there are more species of microlepidoptera recognized in North America than there are subspecies of birds and mammals combined; and there is no reason to suspect that the proportion will prove atypical when our knowledge is extended to the world fauna.

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VI. THE SUBSPECIATION OF SPEYERIA ATLANTIS

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[The Symposium paper on the subspeciation of Speyeria atlantis (Edw.) was presented with the aid of illustrative Kodachrome slides showing examples of the more distinctive geographic races and intermediates. Bereft of extensive illustration a somewhat different approach becomes necessary in preparing a report for News readers.]

The tangled skein one has to deal with in studying and discussing a widely dispersed and tremendously variable species like atlantis is a matter which does not lend itself readily to purely verbal illumination, unless the reader himself can supply an acquaintance with the material and the problems. However, since so little is available in the literature to summarize what appear to be significant intergradations within the Speyeria complex, a summary of the continental gradients of atlantis may be of interest to some, if not wholly lucid to the lay reader. Statements as to "what", "where", "in what direction", and (incautiously, perhaps) occasionally a "why" and "how" are given below, representing my personal conclusions regarding what atlantis is and what it does in North America.

One might say first that this problem is indeed an ecogeographic one; for, unfortunately, the only known structural characters which are helpful in delimiting this species (uncus of male genitalia tapers gently to a ventrad-curved claw without pronounced ventral excavation in the lateral outline; female bursa simple, long ovoid, not compound) fail to separate atlantis from its closest relatives. By genitalic grouping atlantis falls in the callippe

series which also includes zerene (Bdv.), coronis (Behr.), egleis (Behr.), hydaspes (Bdv.) and mormonia (Bdv.). [The species edwardsii (Reak.) falls here, also, but is distinct by reason of the abnormally lengthened superior valve process. One might pry off mormonia, too, because of the delicacy of the male venation: this last character is minor and yet it is tangible, ranking as a good morphological feature.] But even if the student learns to use these helpful structural differences, it is discouraging to have to admit that being left with atlantis, callippe (Bdv.), zerene, coronis, egleis and hydaspes ends the key with the major difficulties in Speyeria still unresolved. Informed naturalists know that these species occur with intricate overlapping at the same flower heads while maintaining everywhere a discrete existence in nature in gradients recognizably different from each other, so the matter of defining the valid species becomes one of following these gradients here, there, and everywhere they go, seeing now this species, now that, varying here gently, there abruptly, dependent upon geography and accompanying ecology. And so, to know species in Speyeria one must learn both their local limitations of individual variation within colonies and also their continental aspects of distribution and fluctuation from this race to that, with all that is thereby implied of the necessity to have good geographic coverage so as to be able to see the intergradations between regionally distinct subspecies.

Quite fortunately, atlantis is classically and nymotypically from the East, where it can have co-existence only with the species of the distinctive

Semnopysche complex [cybele (Fab.), aphrodite (Fab.), and diana (Cram.)] and with the gaudy and altogether unique idalia (Drury). So, we can start with something that is beyond all doubt a valid species, and we find in eastern material a clue to further delimitation, namely, an ecological peculiarity: this species is partial only to the Canadian Zone, being abundant in a continuous geographic sense only in northern New England and Canada, while becoming discontinuous along the Appalachian "islands" southerly to Virginia.

The collector with abundant material finds that eastern atlantis varies considerably more than is generally known. Since the eastern series has absolute characters to separate it from sympatric congeners the variation can be studied as an index of the amount of color fluctuation to expect for a given amount of ecogeographic differentiation. That is to say, in the East, Canadian Zone conditions are rather monotonously similar from Virginia to Labrador and from Cape Breton to eastern Manitoba if judged by the standards one has to use in the West where, in a day's drive, ecologic contrasts (greater than anything known in this huge Eastern territory) ranging from Sonoran to Alpine may be encountered. Of course there are considerable local differences in the East, and yet we have no really severe natural barriers nor abrupt discontinuities. Thus, from the viewpoint of "gene flow" it is not surprising to find that eastern atlantis is more remarkable for similarities than for differences. There is a gradient ("cline") northerly toward brilliancy of silver and increased melanism, along with diminution in size. The Newfoundland material shows some constant differences [canadensis (dos Passos)]; the Shick-Shock (Quebec) colonies are perhaps recognizable as a minor strain; Labrador, Quebec, Ontario, and central Canadian localities support considerable local discal melanism [hollandi (Ch. and Ch.)] but these are not sharply different races.

There are four characters by which eastern atlantis may be seen as a rather homogeneous population with geographic opportunities for genetic interchange so that "wild" mutations have been sifted out and kept within bounds by selection operating under similar conditions. These characters are: (1) constancy of silver: no unsilvered Eastern individuals are known; (2) constancy of dark wing-borders above, heavy and fairly solidly black; (3) relatively narrow limits of variation of the band in the secondaries below, with no outstanding changes in color or encroachment of suffusion; (4) fairly stable coloration of the disk of the secondaries below, this being notoriously variable in the genus: in eastern atlantis the disk does not vary extensively and can be described quite briefly under only three "lines of departure", these being toward a reddish brown, a blackish brown, and an olivaceous overcast.

It has been known for many years that certain individual Colorado specimens looked so exactly like Appalachian individuals of atlantis that nobody, not even the most expert, could tell them apart except on the basis of the locality labels. In this generation a combination of events has lead

us to accept the idea that atlantis does indeed occur in Colorado. Since this is a crucial point (once we have a beachhead in Colorado the variation in and leading out of that state gives us the keys to the continent, so to speak), further elaboration is in order. The principal stumbling-block is that in this western state the web of variation fanning out from the atlantis-like types leads in final phases to insects a world removed from anything ever seen in the East, from brilliant silver to no silver at all, from wide, pale bands to wholly suffused secondaries, from light bright reddish to dark brown and to sordid dark brick-colored disks, from heavy dark borders above to borders with scarcely any suffusion in the interspace between marginal lines.

The first requisite to understanding these appalling variations, material taken in quantity from a large number of spot localities, has only been available in recent years, and at the same time the factual background for a philosophy to rationalize these differences has been slow in building up through the synthesis of recent studies in genetics, ecology, and systematics. In Colorado, and in the other Mountain States where variation in Speyeria is greatest, there is a huge area of Canadian Zone "islands" chopped up by a multitude of barriers of various strengths. Here, the potentialities for dispersal of atlantis are limited not only by its zonal preference but also by its peculiar "stay-at-home" habits which many students have remarked upon. Although a robust butterfly and of vigorous flight it does not stray around in anything like the manner in which the vanesid butterflies, for example, are known to do. This whole region is ideal for the development of local divergences in a butterfly with this sort of behavior. At the same time the isolations are rendered imperfect because the barriers are not so severe but that we may allow for occasional windblown strays and accidentals. These intruders no doubt act as distributors of the small mutations constantly being fixed by selection pressure in the various partially isolated strains. Thus we have it that the "pot is kept boiling", and boil it does, as the Speyeria student is well aware. This is not a complete explanation of the "why" but it is a simplified rationalization which seems to stand the test of examination from various angles. For example, as atlantis is followed out into regions where ecology and geography differ by giving fairly complete or absolutely complete isolation or to extensive areas where conditions of environment are everywhere similar, there is a sharp drop in the extent of variation displayed by the material. This suggests that when left severely alone the western populations thus isolated settle down to a fixity of type comparable to that achieved by the Appalachian spur.

For whatever the reasons, it can be shown that from spot localities in Colorado series of atlantis give all intermediates between the various "forms", with, for example, full intergradation through silver to no silver, wide bands to suffused bands, brown disks to brick-colored disks, and so on. And when, as in the Front Range, we trace these combinations leading through electa (Edw.) into hesperis (Edw.), or, as in the Grand Mesa area, from electa through to nikias (Ehr.), or to various unnamed ex-

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tremes, we are establishing the relationship of an "atlantis" color form to color forms significantly different, from which we can "step again" even farther as we tour the West.

In going Southwest, through southwestern Colorado into New Mexico and Arizona, we find the material varying away from the dark Front Range (hesperis) strains, encountering reddish, light-colored brilliantly silvered phases (nikias). We cannot expect a perfect linear gradient. Occasionally a nikias crops up far to the north in a population predominantly of the hesperis type, with the converse being true, also. We find, dependent on where we collect in and around the melting-pot area: (1) regionally typical color forms within which other phases occur sporadically; (2) a rough balance between two dissimilar types; and (3) continuous clinal variation from Alpha through Omega. From a situation of this sort the systematist retreats as gracefully as possible and is happy to let the geneticists take over.

With dorothea Moeck in the Sandia Mountains of New Mexico we first encounter the consequences of the geography as the Canadian Zone "islands" become wider separated with increasingly severe barriers. Down the San Juans, Sangre de Cristos, and other southerly reaching spurs of the Colorado Rockies, variation progresses but carries some genes from the north. The race dorothea strikes the eye with the impression that here there is but little contact with the things which have gone before. Instead, although dorothea is a "something" in its own right, we can in selected individuals match (fairly well although not absolutely) the other "something" in Arizona which collectors know as nausicaa (Edw.), and of the Colorado types can match only selected southern Sangre de Cristos nikias. No hesperis of "atlantis" are seen; this transition took place farther up the line. Typically, the nausicaa down at the end of this gradient are distinctive, with bold reddish color above (matched in dorothea), large size (also matched in selected dorothea) a slightly more falcate male primary and a secondary disk sprinkled with an overlay of violaceous scaling, and are notably free of extremes of variation (although one specimen is known, data beyond suspicion, to show that even as far away as in Arizona the "atlantis"-like coloration has not been completely submerged).

A further indication that nausicaa affiliates with atlantis is seen in the Grand Canyon area subspecies schellbachi Garth, recently named. This is intermediate from nausicaa to chitone (Edw.), the latter being a southern Utah washed-out version of hesperis with quite evident relationship back to the Colorado storm center. It is probable that the Southwest still holds some secrets, but the material now available from scattered colonies tells us a story of isolated microsubspecies through which nausicaa of Arizona anchors firmly to a gradient stemming from Colorado atlantis. A lot could be said here which must be omitted for reasons of space. Let it suffice that my personal feeling is that these isolated Southwestern "abnormalities"

are exactly what we might expect from considerations of past and present geographic history, ecology, and genetic theory. Probably much of the subspeciation in Speyeria as we know it today has come about in the past ten thousand years consequent upon the last glacial retreat and the climatic readjustments in its wake.

Leaving the Southwest, and before picking up another major line of dispersal from the Colorado center, it is perhaps best to dismiss a few "dead ends". The material from the Nebraska canyons is similar to hesperis and ends against the barrier of the Plains. The South Dakota Black Hills, isolated as they are by bad lands, have a population similar to hesperis, but in series fairly distinct. Here again, as in Colorado, eastern-type individuals occur as rarities in colonies overwhelmingly Western in facies. This happens over a surprisingly large area, from New Mexico to Idaho, and if we try to make a separate species out of it it certainly does not accord with the way argynnid species vary, skulking along with various dissimilar races all over the map. This Appalachian phase is common in some parts of Colorado, but in some places it is very rare and at the same time very different from the associated "atlantis" variation. It would seem that the most plausible explanation is a genetic one, i.e., that the particular combination which we term "atlantis" now and again breaks through the odds built up against its appearance in the various partially separately evolved gene-systems of Western strains. In any event, the Black Hills series, even with the tell-tale Eastern phases removed, still show excellent relationships back to the Colorado series.

The Plateau and Great Basin gradient west from Colorado works away from hesperis, varying principally toward pallidity. The changes in Utah are not radical; affinities are obvious. In Nevada the main-traveled highways cross the ranges in passes too low for atlantis. It is very likely that if these ranges can be tapped at the 9-10,000 ft. elevations we will come into knowledge of something new and strange. Certainly the ultimate, far beyond what one could reasonably expect even in Speyeria is achieved in the East Humboldt and Ruby Ranges in the astonishing race recently named atlantis greyii by Moeck. Here is a population with very little left to show its tie back to mother atlantis. Now and again one finds a specimen brown enough to match Utah material, by selecting the most pallid individuals. The average is unbelievably pallid, resembling Utah S. zerene platina (Skin.). [We must keep our species and races in mind and remember that by the time zerene platina gets out in the Rubies it is yclept zerene cynna dos P. and Grey and is analogously pallid, is in fact, in this same locality with greyii the absurdly extreme end of the zerene possibilities, in just the same fashion that atlantis here goes off the deep end toward unrecognizability.] It is probable that correlation between variability and degree of isolation, the "Sewell Wright effect" of "drift" in small populations, is here as well demonstrated as one could rightfully expect.

Starting anew from Colorado and skirting west of the Divide toward the Northwest, we can follow another long and interesting gradient. Taking a sample from the Teton Mountains in Wyoming we find that we can match selected Colorado and Wyoming individuals but that the drift is away on a fresh slant. Sampling again in the Targhee National Forest region of Idaho, it will be found that it is easy to match the Teton Mountain individuals but increasingly difficult to find a good "hesperis" in what is still rather wide variability. And, again, at the other extreme of the Targhee gradient it is not difficult to pick out specimens which we meet as a predominating type in the Sawtooth Mts. And once we are in the Idaho Sawtooths our catch is unmistakably sicklied o'er with the aspect which in Oregon we call dodgei (Gund.) and which when we find it in the Sierra Mts. of California, only a trifle lighter and redder, we recognize instantly as the classical irene (Bdv.). Yes, it is a long jump from irene to hesperis, and the end products are different appearing insects. Also, along the way, the variation is simmering down and achieves in the end a fairly constant type in the Sierras from which the wild mutants have been weeded out, just as has happened in the Appalachians and in the Far Southwest. The thing in the Tetons, recognizably different from hesperis (generally unsilvered, much band suffusion) the student will see relates to hesperis by reason of the outcrop of numerous "Colorado-like" forms at one end of the gradient. The other end of this tetonia dos P. and Grey gradient ties in similarly with the eastern Idaho variation. Once we get to viola dos P. and Grey in the Sawtooths, as has been said, it takes no skilled eye to see where we are being led.

Since we first called attention to the intergradation from hesperis to nausicaa and from hesperis to irene, a few years ago, students have been quick to see and admit that however these spectacular Southwestern and Northwestern divergences may wear their hue with a geographical difference, their ties back to mother atlantis are really excellent. It is when we turn northward on the last lap to gather up the last major dispersal, that the plot really thickens and we may find some students unwilling to go along with our ideas. Here, taking the end products, we find the horrible situation that in the Manitoba Riding Mountain area there is a very light and rather small extreme of the prairie lais (Edw.) and that we propose fitting this dennisi (Gund.), so-called, into our motley array stemming from hesperis. Also, to make it really interesting, along with this dennisi in the Riding Mountains, partly distinct in ecology but overlapping at the same flower heads we meet again with eastern atlantis in the dark phase hollandi! How can we account for this?

Let us turn west from Manitoba, sampling the prairie lais as we go, finding them a trifle larger and darker in Saskatchewan, still darker in Alberta. But see what happens when we hit the Rockies and again at the northern prairie fringes and in general whenever we get to a fringe of the extensive lais population: the lais elements stay with us, in occasional specimens, but we are being deluged with forms which look intermediate toward at-

lantis and now and again with specimens which could have been taken in the Catskill Mts. This story is altogether too long to tell in detail here and we still do not have enough material to be sure of our facts. The problem of understanding which distinct strains we have funneling into and around the periphery of the Canadian prairies will keep us busy for another generation at least. Where do they hybridize, where do they keep distinct, what are the mechanisms at work? A look at the map should convince one that there is a lot of geography involved and a thought about genetic processes makes us realize the complexity we recognize but cannot yet describe with confidence. We see too many hints of overlap, which cry too loudly to be ignored. One thing does stand out rather clearly, that the variation in northern Montana and on to the Banff region in Alberta suggests very definitely a gradient from hesperis to lais, one which no fair-minded observer with extensive material could deny. It looks as though the lais of the prairies was an end-product in a specialized type of Canadian Zone in which hesperis mutated as it came up behind the glacial recession. Perhaps it practiced with a bit of pre-adaptation in camas prairie pockets along the way, as suggested in the intermediate Montana series.

But how can we explain away the coexistence of dennisi with hollandi in Manitoba; can we have two subspecies in one place? Certainly the rather extensive material studied from the Riding Mountains suggests that hybridization does not occur between these forms, so far as we can guess from dried material. It would be but one more in a long and ever-growing list of known "ring distributions" if we conclude that the Appalachian spur, isolated by the warming of the Mississippi Valley from the Rocky Mountain stem, has worked north and west to this reunion with its kindred. These kindred have apparently similarly followed north and east, where Canadian Zone has become established and where recent separating water-barriers have dried away to permit this meeting of end-products from East and West. Apparently the genic build-up has gone to the point where the twain will not now mingle although through long series of intermediates, going back to the Appalachians and back to the Colorado Rockies, we can end up with individuals inseparable to the eye.

Of course, we are finding out things all the time which may shed light on our troubles. The light prairie lais type goes down the Columbian Plateau into Idaho, where from Genesee we have series similar to dennisi not too many miles away from mountains where viola is a subspecies in another dimension, so to speak. And again, Hopfinger, at lower elevations in the Cascades, not a long distance from dodgei country, turns up individuals reminiscent of Colorado hesperis (!) and occasionally one light enough to match Canadian lais. It is questionable if these "lais" colonies would hybridize with the dodgei-viola mountain cline, even if geography and ecologic preference would permit, which in this case they do not. Students of North American butterflies are just beginning to realize how irreversibly and how far along the path toward a separate evolution the subspecies of polytypic species can drift with the aid of isolation and resultant

SUBSPECIATION SYMPOSIUM. Grey: Speyeria atlantis - concl.

slight changes in genetic constitution.

For the facts as we know them now, Occam's razor seems to be our best interpreter, cutting through to accept the simplest explanation consonant with our material and with the geography. We do find a welter of variation wherever barriers are sharp and yet not severe enough to prevent their being breached often by strays, and we find that from a Cordilleran center where variation is greatest we lead out to divergences and end-products which have little conspicuously in common with "atlantis". So, this butterfly shows us both the results of intermingling

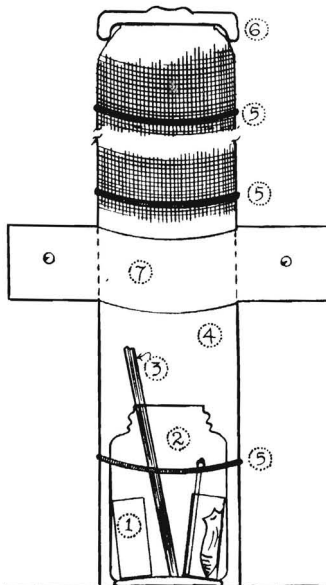
strains and of divergency. But the assumption that this is a continental species is a simple one and seems to cover the field, allowing for everything. If we find that the simple premise leads to elaborate conclusions, or even to spectacular things like ring distributions, it may be because the story of subspeciation is intricate and wonderful in many ways which the earlier workers never suspected. Nevertheless, the material we have is so varied, and is at the same time so intermeshed, that it seems presumptuous to suppose that future explorations will have nothing to add in the way of novelties, intermediates, and modified theories.



AN APPARATUS FOR INCUBATING LEPIDOPTEROUS LARVAE OR PUPAE IN NUTRITION AND ENVIRONMENT TESTS

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The following description of apparatus applies to incubating pupae of Papilio ajax L. (= polyxenes Fab.). It can also be used for rearing larvae. The parts referred to by number are shown in the diagram.



Each pupa is detached from its place by cutting through the girdle and the cremastral silk and is placed in a 'homoeopathic phial' (1) measuring 1 3/4 by 5/8 inches. Seven of these phials will occupy a jar (2) of 6 fluid ounces capacity, 4 inches high (outside) with mouth 1 1/2 inches diameter (inside). The phials should be inserted or removed by means of wide curved forceps. A narrow strip (3) of lath or pasteboard, 1/2 to 1 inch wide and 5 inches high, must rest between the phials to give the emerging adults a rough surface to grip on their way up.

The jar is to be surrounded by wire gauze (fly-screen), rolled to make a cylinder (4) 3 inches in diameter and about 18 inches high; the cylinder is made to keep its shape with three elastic bands (5). At the top the cylinder should be compressed to a diameter of about 2 1/2 inches, to support the loose lid of a quart 'sealer' jar (6) so that it overlaps the wire. Each cylinder must be attached loosely by a broad paper band (7) held by thumb tacks to a board or the edge of a table, so that it can be slid up and down, operations that must be done to remove the jar for recording from which pupa an adult has emerged.

The butterfly climbs to the top. A cylinder of 3 to 2 1/2 inches diameter is recommended for experiments with Papilio ajax, wide enough to enable the wings to expand fully and narrow enough to discourage fluttering. Chilling also discourages fluttering.

For rearing larvae, the jars have a wire gauze cover through which, by enlargement of holes, plant stems are passed into water or solutions being tested. The plant should be pulled down from above by the stem into the cylinder, the lower 4 inches of stem being free of side twigs so that it can pass through the gauze cover; pushing the plant upwards tears or bruises the succulent leaves and twigs.

The following advantages may be claimed for this kind of apparatus. Jars of these dimensions do not occupy much space. They can be closed so that the pupae can be incubated under controlled relative humidities, or exposed to the influence of gases or volatile chemical compounds, or to different temperatures; after the required intervals of time the jars can be placed in the cylinders. For controlled humidities the operative fluids (e.g., KOH solutions of known specific gravities) are placed in the jar; a platform of glass-wool or beads can be used to support the phials. One advantage of such an apparatus for rearing larvae is that the frass falls to the gauze cover or to the base where it can easily be removed for analysis or any other purpose.

The entomology of Holland and Indonesia suffered a great loss with the tragic death of Prof. Dr. L.J. Toxopeus, who was overrun and killed by a motor car in Bandung, Java, on 21 March 1951, 56 years of age.

In him we lose one of our best entomologists, an eminent lepidopterist who was an authority on the fauna and the zoogeography of Australasia, a specialist of Rhopalocera, especially of Lycaenidae of that region, an unrivalled collector, the soul of the Entomological Society in Indonesia, and the author of numerous publications on Lepidoptera.

Lambertus Johannes Toxopeus was born on 8 September 1894, in Toeban, Java, of Dutch parents. He studied biology at the University of Amsterdam. The studies of the zoogeography of the Malay Archipelago by the eminent Amsterdam zoologist, Prof. Max Weber, made a deep impression upon him and influenced the choice of his specialization: zoogeography of the Australasiatic region tested upon taxonomy and distribution of Lepidoptera. Long before the taking of his final degree he had already taken part in the Expedition to Boeroe (Moluccas) in 1921, as leader of the Zoological-Botanical section; his zoological collections provided material for a great number of papers published in *Treubia* under the joint title "Fauna Buruana" running up till now. In 1923 he was appointed teacher in Natural History at Amsterdam. In 1930 he took his D.Sc. degree on a thesis titled "The Species as a Function of Place and Time tested upon Lycaenidae of the Australasiatic Region", a pioneering study in which he formulated the principle of his *species duplex*, at the present time recognized and adopted by several zoologists. Unfortunately, this study was published in Dutch, which is the reason that it remained little known. His ambition of later years was to revise and republish it in English, but the war, his manifold interests, and his teaching prevented that.

Subsequently Toxopeus - "Tox" to his friends - went to Java in the same year, and was attached to several secondary schools, at Bandung, Batavia, and Buitenzorg. His spare time was entirely dedicated to zealous collecting and field observation during numberless trips in Java, Sumatra, and Celebes.

In 1938 he was appointed by the Government of the Dutch East Indies leader of the Dutch group of the Third Archbold Expedition to New Guinea 1938-39 (also called the joint Netherland-Indian-American Expedition), and collected insects in the Snow Mountain region for one year. These collections of insects were enormous, unrivalled, the richest we ever saw; the enthusiasm of every specialist concerned with their study is unanimous; many decennia will be needed for the study of this material. After the expedition, Toxopeus was attached to the Zoological Museum at Buitenzorg for two years, in order to assist with preliminary study of these collections. After the Japanese invasion he was taken prisoner of war, and after the capitulation of Japan sent for

* "De soort als functie van plaats en tijd, getoetst aan de Lycaenidae van het Australasiatisch gebied", 198 pp., 17 text figs., 4 plates, ed.H.J. Paris, Amsterdam, 1930.

one year to Europe on a convalescence leave which he chiefly devoted to study and visits to entomological collections. Afterwards he was appointed Professor of Zoology at the University of Indonesia at Bandung, where he taught till his death. He was chairman of the Entomological Society in Indonesia, member of the Netherlands Entomological Society and since 1948 of the Lepidopterists' Society.

Toxopeus was an unforgettable figure. Very tall and thin, he looked frail but possessed in fact most enviable energy and stamina. Great and highly infectious was his enthusiasm. It was a pleasure to speak to him of any matter or problem; one was always certain to receive his fullest attention and sound advice. His entomological reading was enormous, and his general knowledge of entomology, geography, and history of collecting in South Asia, together with his brilliant memory, brought him the nickname of "walking cyclopaedia". So great was his enthusiasm in collecting and unhemmed his interest for every group of Macrolepidoptera that for years he hardly took time to get down to publication of his knowledge. But in the later years more and more papers came from his hand, and great were his plans for the future. His lamented death interrupted his almost completed study of the Papuan *Delias* which he intended to read before the International Entomological Congress in Amsterdam this summer. He was the most scrupulous and the best collector we ever met.

Always kind and good-humored, an excellent entertainer, he was greatly popular among his pupils, at high schools as well as at the University, amongst his colleagues and his very numerous friends. His so abrupt and tragic end leaves a gap which never can be filled. Our sincere sympathy goes to his wife and seven children.

A. Diakonoff



One of the best known British amateur lepidopterists, HENRY JEROME TURNER, died 19 December 1950. He was born 27 August 1856. He was a schoolmaster of the Denmark Hill School for many years and eventually became Headmaster. Turner was a devoted disciple of J.W. Tutt and succeeded him as editor of the *Entomologists' Record* in 1911 at Tutt's death. For many years he published little supplements to Tutt's "Varieties of the British Noctuae". His largest single work was *Butterflies of Cyprus*. In spite of a very large number of short papers he did little original research. He was most devoted to his editorial and organizational duties. Turner was elected Honorary Life President of the Royal Entomological Society of London in 1944 and Special Life Fellow in 1948; he had been Librarian for some years beginning in 1921. He was Editorial Secretary of the South London Entomological Society for about 40 years, beginning in 1894. N.D. Riley wrote of him: "A little man, bolt upright and of rather rigid views, Turner was every inch a schoolmaster and had been a figure in London entomological circles, and internationally, for more than sixty years when he passed away, still at work, on December 19, mourned by a very wide circle of friends."

A COORDINATED STUDY ON THE MIGRATION OF THE MONARCH BUTTERFLY:
A PLEA FOR INFORMATION FROM LOCAL NATURALISTS

by Geoffrey Beall
University of Connecticut
Storrs, Connecticut

1. INTRODUCTION

When one goes to some new part of America, one may find that significant information on the migration of the Monarch Butterfly, Danaus plexippus L., is commonplace to the local naturalists. Such knowledge should be made generally available, coordinated, and put on record. In illustration of the harvest of information that should be gathered, let us consider a simple situation. First, let us note that Williams, et al (1942) has summarized all the migrations of the Monarch, as reported in the literature over a period approaching a century. Now, it is remarkable that no migrations have been reported in certain states, notably in the region midway between the Atlantic and the Mississippi. The gap is so glaring as to raise the possibility that there are two streams of migration, one down the coast to Florida, the other further inland, southwest to Texas or Mexico. What, however, are the facts, if one goes into the "empty" region, as into western Pennsylvania? The writer found that in this state there was a widespread, massive, and universal flight to the southwest in September, 1949. He learned, moreover, by enquiry from reputable and reliable local naturalists that many years such a flight is manifest in that region and in West Virginia during September. He was further told that considerable aggregations of the Monarch occurred by a lake near Pittsburgh and even on a hill-top in the city. Let us say that the situation in the "empty" region reflects more unfavorably on the inhabitants than on the Monarch Butterfly. Although, what could the local naturalists do with their isolated bits of knowledge in a field not of pre-eminent interest to them? Hence, we plead that they contribute such information to the Lepidopterists' Society for a grand assembly.

Readers of the Lepidopterists' News may well observe at this point that Danaus plexippus is already getting reasonable attention in the study on "The Nearctic Butterflies", in the "Field Season Summary", in certain special studies afoot to mark and recapture it, and in miscellaneous notes. To this we may first object that, as will appear below, we are interested in other aspects of the problem. Secondly, we make an especial claim for the Monarch to detailed study. It is THE MIGRATING BUTTERFLY, par excellence; it is easily seen, easily identified, and moves by day. If we knew better the details of its behavior perhaps we could more effectively study the movement of other less conspicuous insects.

The kind of record that might most usefully be contributed by local observers will be indicated below. The matter may, the writer hopes, be helped forward by a brief summary of some of his own endeavors with suggestions that further and wider observations of the same kind be made and reported.

2. WHAT IS THE TREND OF FLIGHT IN VARIOUS DISTRICTS?

The greatest contribution that could be made by local observers is the very simple one of reporting the trend of flight in various places over the continent. By this we mean, for instance, that they should have reported the fact that during the first two weeks of September, 1949, the flight in the region of Pittsburgh was steadily and strongly to the southwest. If 100 observers, in various parts of the continent, had made such a report during that September, we should have a map like that of the meteorologists and see where the currents of Monarch Butterflies were flowing. Perhaps such a map would only rival that of Williams if it were made up for September. If a similar map were, however, made up for June it would throw light on a period about which very little is known or can be known from the present approach to the problem - although as will be pointed out below a different approach could guarantee results. A similar map for the mid-summer might show northward movement in some parts of the country and southward movement in others so that we should be a little nearer the question of what decides the direction of movement.

It will be wise to warn any potential observer of what, in the way of flight, he should not expect to see. It will be further judicious to set forth in some detail how data on flight should be collected, compiled, and interpreted.

Let us note again that the flights that have been reported in the literature and summarized by Williams are great and massive flights such as merit note even in a local newspaper. Any observer may be so fortunate as to see such flights, but in these we are not unduly interested. We are interested particularly in the general trend of flight that is obvious to anyone who is in the field but which, let us say, merits no notice in the popular press. We are further interested in the total movement of the many single butterflies that can be seen from time to time, even in a season when they are scarce.

The remarks just made are necessary because the study of insect migration had an unfortunate start. In the first place it tends to be shaped against the background of the migration of birds. The questions asked usually presuppose a similar mechanism for birds and insects. People are anxious to prove, say, that the Monarch Butterfly does remove entirely to the south and then return. They want to know whether individuals do this, like birds, or whether successive generations do it. The migration of butterflies is not necessarily like that of birds, however, and there is presented briefly below some evidence that it is actually quite different. In particular, whereas birds interrupt their residence in either the north or the south to move briefly to the

other place, the Monarch seems to be always on the move, one way or the other. In the second place the casual nature of most records on insect migration has tended falsely to associate the movement with abundance of the insect because of its sensational character. The literature on the Monarch, and other insects, constantly reports the occurrence of great bands which are probably not truly bands but casual concurrences of great numbers of butterflies.

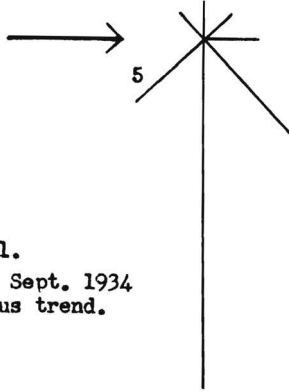


Fig. 1.
Flight on 13 Sept. 1934
with obvious trend.

The reader may justly ask what the writer meant by saying there was a widespread and obvious trend to flight. The phenomenon can be illustrated with Fig. 1, which shows the number of Monarch Butterflies that passed during a single hour through a glade in Ontario, on 13 September 1934. The record is in the form of a rose and shows that there were 5 Monarchs going to the southwest, 19 south, 7 southeast, 3 east, 2 northeast, 2 north, and 2 northwest. There was clearly an overwhelming preponderance of movement to the south - yet butterflies being what they are, a few passed northward through the glade. Note that these butterflies were moving alone, one or at most two at a time, although the total effect was of unanimity to the south. Such records could be obtained very easily and regularly near Pittsburgh in September, 1949. Will local observers make such observations and fill up the empty states between the Atlantic coast and the Mississippi? There is no need to wait until great and spectacular flights are observed. Will others discover, during the autumn of 1951, how the Monarch flight tends in the eastern Gulf States? Do the Monarchs flow towards Texas or Florida? The question could be so easily answered. Is the trend of flight in the western part of the Carolinas towards Florida?

We have declared ourselves interested in the total movement of the many single butterflies that can be seen from time to time, even in a season when they are scarce (in contrast to the situation on 13 September 1934). This is a matter similar to that just discussed but requiring more patience and yielding even more valuable and unexpected information. The writer and some co-workers accumulated a number of such records on each Monarch and its direction of flight at Chatham, Ontario, which is near Detroit. The results for the period, July 1 through August 10, for the years 1935 through 1940, are summarized in Fig. 2. For this period, it can be seen

that there is a preponderance of movement to the north and west. It should be realized that only occasional single butterflies were involved; no one would have reported any movement at all, by casual observation. The possibilities of such an investigation will be better appreciated when, below, we come to the question of such trends of flight throughout the year.

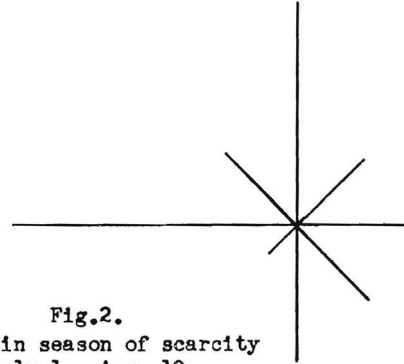


Fig. 2.
Flight in season of scarcity
July 1 - Aug. 10.

Any very extensive collection of data, such as those of Fig. 2, raises a problem as to how we may summarize more concisely the nature of flight. How are we to determine definitely and objectively the general trend of flight to the north and west? This problem may be solved by the numerical technique that we would use in physics to find the net effect of forces pulling in various directions. This elementary numerical technique may be familiar as the "polygon of forces". When the result, which is called a "vector sum", is divided by the total number of butterflies involved, we get both a measure of the direction and of unanimity of movement during the period in question. The whole matter has been discussed at some length by the writer (Beall, 1941). Let us not concern ourselves unduly with the technique except to note that it exists and provides a neat summary of results. Let us further note that if anyone collects the data, the analysis of the type indicated will most gladly be made for him. Send the data to Dr. Charles L. Remington or to the writer.

If the reader is prepared to think now of accumulations of data, like those of Fig. 2, but wishes them resolved into net movements let him consider Fig. 3. The direction of the net movement is indicated by the direction of an arrow. The unanimity of the movement is indicated by the length of the arrow. In such terms, Fig. 3 indicates the flight for various seasons in southwestern Ontario. The seasons were as follows:

- (1) Earliest spring through June 30
- (2) July 1 through August 10
- (3) August 11 through August 24
- (4) August 25 through September 7
- (5) September 8 until the latest autumn.

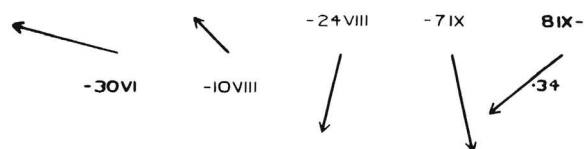


Fig.3. Net movement in various seasons.

Two effects are important. The first is that the unanimity of flight to the northwest in the spring is as great as that to the southwest in the autumn. It is strange to see that the flight is so unanimous before August. In this early period, before the butterfly has become abundant, it never attracts much attention and migration is hardly noted, and only in a casual way. Secondly, it seems that migration flows continuously and turns like the tide, at a certain critical period early in August. All spring and early summer it flows towards the north but in late summer it turns to the south and continues flowing that way all autumn. During the winter, it may even have its sluggish trend in California or Florida.

The local naturalists, to whom the present appeal is addressed, might in the spring of 1952 determine in a similar way the trend of flight in many parts of America. These results, when conjoined and plotted, would produce a map showing how the currents of Monarch migration flow in the spring. Such a picture would be very handsome without any appeal to the usual questions of whether the Monarch behaves like a bird in migration. It could, moreover, be undertaken with the advantage of guaranteed success, because it depends only on the event of seeing individual Monarchs - not on the chance of seeing some great and spectacular flight.

3. THE RECAPTURE OF MARKED MONARCHS

Current plans by certain members of the Lepidopterists' Society to mark very great numbers of butterflies, in the hope of their recapture, may fit together very well with evidence of the kind recommended above. The writer does not propose to deal at any length with this question but merely to say that he is most sympathetic, will cooperate, and urges local naturalists to examine all possible Monarchs for markings, which should be reported to Dr. Remington.

4. UNDER WHAT CIRCUMSTANCES DOES THE MONARCH FORM CLUSTERS?

The topic which the writer emphasizes, *i.e.*, that of trend of flight, is one that can be rather readily discovered by local observers and discovered only by them. There are, however, minor investigations on which we should perhaps touch. One of these is the question of the circumstances under which clus-

ters of the Monarch form.

Let us note, in a general way, that the Monarch frequently attracts attention by its tendency to cluster on trees at night. This clustering, so frequently described in the literature, is again the grandiose phenomenon and worthy of the local newspaper. Nevertheless, the much less spectacular but biologically significant smaller clusters should also be reported. The writer has only once seen the great spectacular clusters but on the other hand he has seen clustering of the minor variety hundreds of times. One can see such clusters almost any day in early September on the capes or peninsulas along the northern shore of Lakes Erie and Ontario. There are undoubtedly other equally favorable situations in America. It should be noted, in passing, that it has commonly been supposed that these clusters regularly and only form in migration. In actual fact, they form only when a number of Monarchs happen to find themselves near one another in the evening, and they seem to form in the summer if such a coincidence of butterflies occurs.

It is becoming clear that coincidences of population sufficient to produce clusters occur most frequently when flight is barred by lakes. There is a suggestion, however, that they also tend to occur on hill-tops.

Observers, like those in the vicinity of Pittsburgh mentioned above, are in a position to report many clusters of the "minor" kind. Twenty or more Monarchs on a given tree are worthy of report. The naturalist should note briefly the circumstances: whether the clusters are beside a lake and if so on which shore; whether they are on a hilltop and if so their disposition with regard to wind; if they are elsewhere and if so whether the trees stand beside an open space and what the wind direction is.

5. HOW DO SEX PROPORTIONS VARY?

A second lesser point that may be conveniently studied by local observers is that of variation in sex proportions during migration. In illustration, we may consider a curious phenomenon that occurs in Ontario during the great autumnal migration. The situation may be illustrated by data (Beall, 1946), as follows:

1 September 1940 - 39% female
7 September 1940 - 47% female
14 September 1940 - 63% female

It can be seen that the proportion of females rose regularly, week by week, during this period. Such seems to happen every year, although why is not clear. It would be illuminating to see if this effect is accentuated in the flight down the continent, as if there were a tendency for males to outfly the females.

The data on percentage of females are based upon very highly representative collections from small clusters from which all the butterflies could be taken for examination. Since all the Monarchs were quiescent there was no question of one sex tending

to escape the net. Any study of sex proportions should be of such resting material rather than of butterflies taken on the wing.

6. SUMMARY OF RECOMMENDATIONS ON OBSERVATIONS

There is a vast amount of data to be collected before we have an adequate picture of the migration of even a single conspicuous species like the Monarch. We may summarize, in order of decreasing importance, the work that may be done by interested local observers as follows:

I. Record the direction of movement of each Monarch seen in fairly consistent flight, the direction of wind, and the date. For any period when a total of 30 Monarchs has been so recorded, it is possible to calculate the net flight and its degree of unanimity. If the reference to this numerical operation, given above, is insufficient for anyone to make the calculations, we will gladly make them if the data are sent to Dr. Remington or to the writer.

II. Record the circumstances of the Monarchs forming clusters - including small clusters down to 20 butterflies. There should be noted the day, hour, and circumstances. In connection with the circumstances, it is important to note whether the clusters were formed beside a lake or on a hill top. If they are formed in some other type of situation, the circumstances should be further described and in particular the direction and strength of wind should be noted.

III. Record the number of each sex if one is dealing (as in studies on recapturing marked specimens) with quiet Monarchs taken from clusters on trees.

The purpose in pointing out the great contributions that local naturalists may make is with the aim of correlating the vast amount of knowledge, which is insignificant in its parts but most important in the aggregate. Accordingly, all correspondence will be welcomed by Dr. Remington or by the writer. As previously mentioned any assistance in numerical analysis of flight data will be most gladly given. We shall guide ourselves by the contributor's desires as to the use made of such data. The contributors will, however, in all probability, usually hope for a report like those distributed by the Lepidopterists' Society on other special studies of groups and regions. It is hoped that such a report can be distributed to the contributors annually.

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PERSONALIA

The vacancy in the Section of Insects and Spiders of the Carnegie Museum in Pittsburgh, created by the death of Dr. W.R. Sweadner, has been filled by the appointment of HARRY K. CLENCH as Assistant Curator, in charge of Lepidoptera. Mr. Clench, co-founder of the *Lep. News*, is a specialist in the Lycaenidae. It is satisfying to learn that the Museum is continuing to keep a lepidopterist on its staff, thus ensuring proper supervision of the tremendous collections assembled by W.H. Edwards, W.J. Holland, A. Avinoff, B.P. Clark, et al.



The issue of the *Journal of the Washington Academy of Sciences* for January 1951 has been dedicated to AUSTIN HOBART CLARK, on the occasion of his retirement as curator in the U.S. National Museum. In addition to a portrait and summary of scientific contributions, there are thirteen papers by friends and colleagues of Mr. Clark, describing new species and genera named for him of: fossil brachiopods and molluscs; and living molluscs, copepods, shrimps, corals, polychaetes, and Lepidoptera (a new *Olethreutid* described by J.F.G. Clarke). [Lepidopterists' Society members will recall that they have recently elected Mr. Clark First Vice President, and that he presided at the first annual meeting of the Society in New York, December 1950.]



M. PIERRE E.L. VIETTE, of the Paris Museum, has been awarded the "Prix Constant" by the Société Entomologique de France, for his distinguished work with the taxonomy of the Lepidoptera. M. Viette left Paris in late August, to spend six months in Madagascar, near Tananarive, to collect chiefly the Microlepidoptera. Very few "micros" are known from Madagascar. M. Viette attended the IXth International Congress of Entomology and the Special Meeting of the Lepidopterists' Society in Amsterdam in early August.

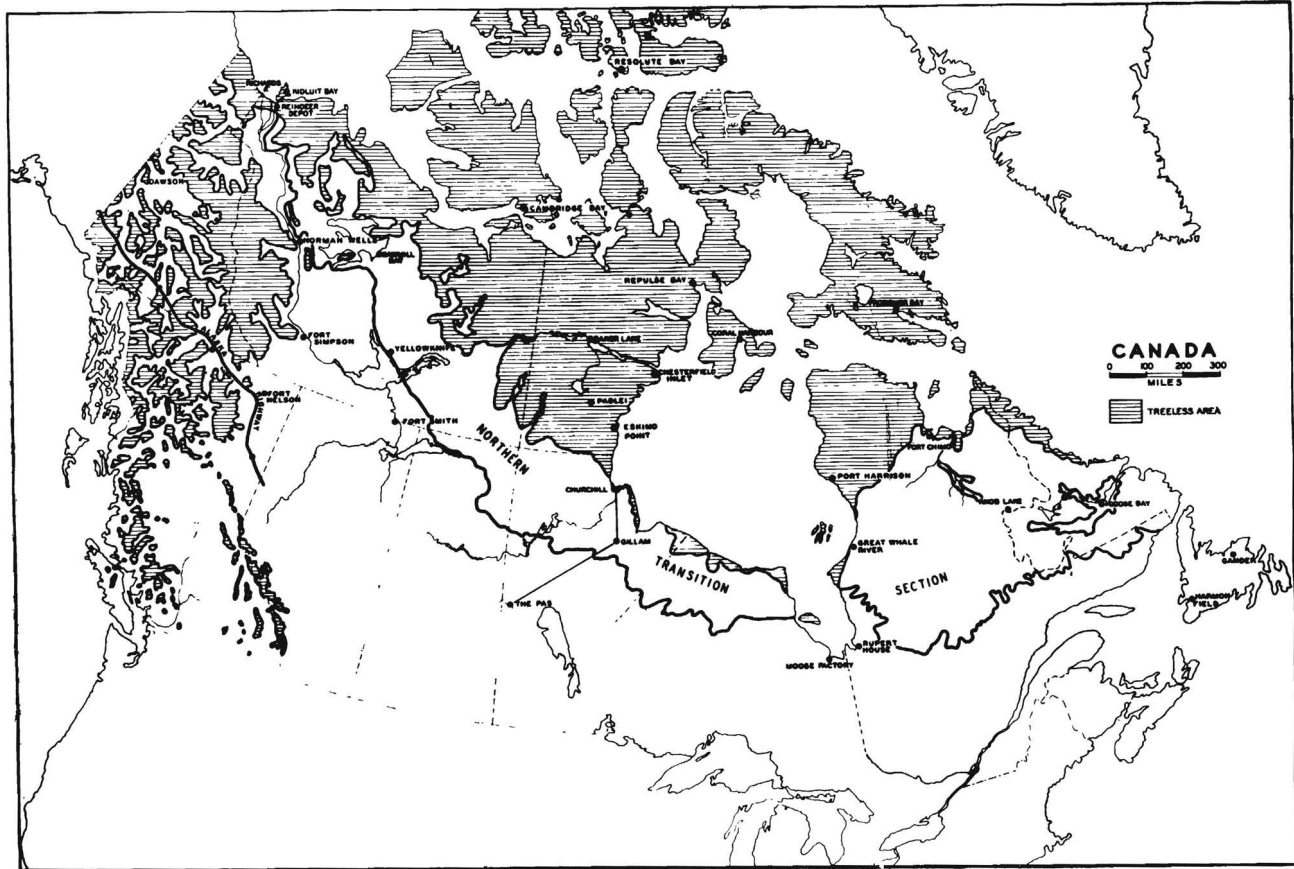


The death of M.N. RIMSKY-KORSAKOFF, noted Russian entomologist, was announced in Moscow 18 March 1951. His voluminous publications included work on Lepidoptera. He was President of the Entomological Society of Leningrad and bore the title from the Soviet Government "Honored Scientist of the Russian Republic". His father was the famous musical composer, Nikolai Rimsky-Korsakoff.



The Collection of the late HAROLD I. O'BIRNE, primarily composed of Missouri Lepidoptera, was recently purchased by the University of Missouri and thus becomes a major feature of the insect collection of the Department of Entomology there. Mrs. O'Byrne has settled in Sierra Madre, California.





Faunal regions of northern Canada and Northern Insect Survey localities.

NORTHERN CANADA AND SOME NORTHERN BUTTERFLIES

by T. N. Freeman
Ottawa, Ontario

The plan of this paper is to outline briefly the faunal zones of northern Canada and mention some of the butterflies characteristic of each. This information has been made available through the activities of the Northern Insect Survey, which has obtained, since it was inaugurated in 1947, approximately half a million arctic and subarctic insects, including about 125,000 Lepidoptera.

The accompanying map (Fig. 1) shows the locations of the survey parties, which were distributed from the Alaska boundary to Newfoundland, a distance of approximately 3,000 miles. The survey covered the Yukon, the vast Northwest Territories, and northern parts of British Columbia, Manitoba, Quebec, and Newfoundland, including Labrador. The localities are situated in the arctic tundra north of the tree-line, as shown on the map, and in the boreal forest south of it. These two zones are characterized by different species of Lepidoptera, which overlap somewhat at the tree-line. We shall call this intermediate zone the northern transition

section. Ft. Chimo and Great Whale River, P.Q., Churchill, Man., Yellowknife and Reindeer Depot, N.W.T., are localities near the borders of this transition section. This distributional overlap is caused chiefly by the presence of islands of tundra within the northern fringe of the trees, and the extension of the forest into the tundra, particularly along drainage systems. The dispersal of a species is also responsible for some transitory distributional overlap. It is peculiarly significant that within this transitional area, where species of the barrens meet closely related species of the boreal forest, there is no evidence of gene interchange between the two. This suggests the hypothesis that phytophagous insects indigenous to the arctic tundra are specifically distinct from those indigenous to the boreal forest south of the transitional section. The following examples serve to illustrate this hypothesis. *Erebia rossi* Curt. is distributed over the barren lands from Reindeer Depot to Baffin Island. In the west, it occurs above timber-line in northern British Columbia. But, in

comparison, Erebia discoidalis Kby. occurs in southern Quebec from north of lakes Huron and Superior to James Bay, from south of Lake Winnipeg to Churchill, Manitoba, northwest to Great Slave and Great Bear lakes and west to Dawson, Yukon. These two species overlap at Churchill and Gillam, Manitoba. The exquisite bouncing-brown, Erebia fasciata Butl., occurs in the barrens of the Northwest, roughly north of a line from Dawson, Yukon, to Padel in the Keewatin District of the Northwest Territories. At Dawson, Reindeer Depot, Coppermine River, and Great Slave Lake, fasciata meets Erebia disa Thun., which extends south to Banff, Alberta; Riding Mts., Manitoba; and Smoky Falls, Ontario, south of James Bay. Other examples of this type of distribution are the barren-land species Colias hecla Lef. and Colias nastes Bdv. which are separated from the boreal forest insect Colias interior Scud. by an inhabitant of the Transition Section, Colias pelidne Bdv. and Lec. Oeneis assimilis Butl. is another barren-land species, which meets Oeneis jutta Hbn. at the timber-line, the latter sphagnum-bog species extending well south into the boreal forest. Other examples are found in the genus Brenthis (or Boloria, if you prefer).

The boreal forest extends almost to the arctic coast near the mouth of the Mackenzie River, and such butterflies as the mourning cloak, Nymphalis antiopa L., and Papilio glaucus canadensis R. and

J. have been collected at Dawson, Aklavik, Norman Wells, Ft. Simpson, and Ft. Smith, localities in the Yukon and in the Northwest Territories. These butterflies are typical of northern United States and southern Canada. I mention this to point out that, if any collector is contemplating a trip to collect arctic species, he may be within a few miles of the Arctic Ocean and still capture butterflies he could obtain near the Mason-Dixon Line. Some of the true arctic-tundra species extend south at arctic-alpine elevations in the Cordilleran mountain system to Colorado. In the east, some extend southward as isolated populations to arctic-alpine regions in New Hampshire.

The arctic tundra, although inhospitable at times, supports countless thousands of specimens of a few butterfly species, and at times it is possible to collect over 200 specimens of a single species in a day. It is rare, indeed, to match this condition in the south.

This is Contribution No.2780, Div. of Entomology, Science Service, Dept. of Agriculture, Ottawa, Canada. The Northern Insect Survey is a joint project of the Defense Research Board, Dept. of National Defence, and of the Division of Entomology of the Department of Agriculture, Canada.

SOCIETY NEWS

The Secretary, Dr. F.H. Rindge, has sent notification of action taken by the Executive Committee, as provided by the Constitution, as follows:

1. THE ANNUAL MEETING FOR 1951 WILL BE HELD IN CHICAGO, ILLINOIS, at the Chicago Natural History Museum (formerly Field Museum), on December 28-29.

2. Article 3, Section 1, of the By-laws has been amended to read as follows:

"An order of business for the annual business meeting shall be prepared by the Secretary in consultation with the President. The remainder of the program for the annual meeting shall be prepared by the Chairman of the Program Committee."

3. Charles L. Remington has been appointed Editor-in-Chief and Librarian.

The Special Meeting of the Lepidopterists' Society, announced in the preceding issue of the News, was held in Amsterdam on 21 August under the chairmanship of Dr. Walter Forster, of München, Germany, Vice President of the Society. The program was devoted to a symposium with the title "The Phylogeny and Classification of the Lepidoptera." The three invited speakers were: Prof. T.A. Wohlfahrt of Würzburg, Germany; M. S.G. Kiriakoff, of Ghent, Belgium; and Prof. H.E. Hinton, of Bristol, Great Britain. Their papers will be published in an early issue of the News, along with the report on the Meeting by Dr. A. Diakonoff, who served as

Chairman of the Organizing Committee. Dr. Diakonoff writes that 750 copies of our tri-lingual program were distributed to the members of the IXth International Congress of Entomology, in conjunction with which we held our Meeting. He also notes that our Meeting was well attended and that "everybody agreed that it was a success."

We received with great pleasure a greeting addressed to the Editor-in-Chief and signed by 37 of the members and guests who attended. The signers represented at least 12 nations on 4 continents.

Society members in Europe will be pleased to know that arrangements have been made with E.J. Brill, our Amsterdam agent since 1949, so that Society dues and News subscriptions may be paid in the following countries in native currency, addressed to Brill as follows - (from all other countries, except Italy, remittance can be made direct by postal orders):

NETHERLANDS: Amsterdamsche Bank, Leiden.
FRANCE: Crédit Lyonnais, Compte no. P.B.C. 11.055, 19 Blvd. des Italiens, Paris.
GREAT BRITAIN: Barclays Bank Ltd., Chief Foreign Branch, 168 Fenchurch St., London E.C. 3.
GERMANY: Postcheckkonto Karlsruhe 44378, in the name of E.J. Brill Verlag, Heidelberg.

Remittances, when in dollars, should always be sent directly to the Society Treasurer.

C.L. Remington

SIMPLE STATISTICS FOR THE TAXONOMIST
(continued from page 6)by F. Martin Brown
Colorado Springs, Colo.

II. INDICES

How often have you seen a statement like this: "The bands on 'A' are wider than those found on 'B'?" In all probability each time that you have seen such a statement you have wondered what the author really meant. You have wondered if you would agree with him that the differences are worth mentioning. You would like to know how much wider they are or better still how wide they are on each member of the pair.

The best way to state such a measurement is as an index. Let me show by a concrete example just how this works. In the course of a study of the variation found in Heliconius charitonius, William P. Comstock made a great many measurements on a large series of specimens. During this study he came to the conclusion that the Mexican series before him represented a population that was different from the nominotypical population from the Virgin Islands. One of the characteristics of the Mexican population as defined by Mr. Comstock is the narrowness of the yellow bands across the forewings.

THE PROBLEM: Are the yellow bands across the forewing of the Mexican population of H. charitonius significantly narrower than those found on H. charitonius charitonius (Linné) from the type area?

THE SOLUTION: Among the measurements made by Mr. Comstock are two that have a bearing on our problem: the radius of the left forewing and the width of the yellow bands on the forewing taken at a standard point referred to the venation of the wing. Table 4, below, was developed from the individual measurements of these characters by treating them as outlined in the first of these articles.

TABLE 4.

Certain Parameters of Two Samples
of Heliconius charitonius

Sample	Width of Discal Band		Radius of Forewing	
	Mexico	Virgin Is.	Mexico	Virgin Is.
N =	84	43	84	43
Mean (mm.)	2.35	2.36	41.81	38.02
p.e.m (mm.)	0.02	0.03	0.25	0.26
S.D. (mm.)	0.26	0.25	3.43	2.53

When we examine the data labelled "Width of Discal Band" it is immediately evident that bands on the two series have essentially the same width. Testing the data we find: difference 0.01 mm.; probable error of the difference 0.04 mm.; "t" score 0.25. With "t" less than 1 we can safely say that there is no difference in the absolute width of the bands on these two series.

Turning to "Radius of forewing" there seems to be a real difference. Testing the data we find: difference 3.79 mm.; probable error of the difference 0.36; "t" score is greater than 10. With "t" so large there is little chance that the difference in size between these series is fortuitous. We can safely say that the Mexican population is really larger than the Virgin Is. population [H. charitonius charitonius].

Since the bands are the same width on the two samples they will seem narrower on the larger insects and wider on the smaller insects. This apparent difference in band width can be stated numerically. It is done by establishing the BAND INDEX for each specimen. The band index is nothing more than the width of the band stated as a percent of the radius of the forewing:

$$\frac{\text{width of band}}{\text{radius of forewing}} \times 100 = \text{band index}$$

The band index takes into consideration the size of the specimen in such a way that if the radius of the forewing is constant the index fluctuates directly with the width of the band, the wider the band the larger the index number. The band index therefore is a concise statement of the relative width of the band. This technique can be used for finding a numerical expression for many types of relative condition. Indices of this sort may be treated as linear measurements and their parameters defined. Table 5 does this for our two samples.

TABLE 5.

The Band Indices of Two Samples
of Heliconius charitonius

Sample	N	mean	p.e.m	S.D.
Mexico	84	5.63	0.04	0.55
Virgin Is.	43	6.37	0.05	0.44

By applying the standard tests to these figures we find: difference 0.64; probable error of the difference 0.06; "t" score is over 10. Again "t" is so

large that there is virtual certainty that the apparent difference in relative width of the bands is real.

REMEMBER THIS: When using indices be certain that the basic measurement used is a fundamental property of the specimens being studied.

[Mr. David Calhoun, biometrician at Yale University, has very kindly reviewed this series of articles and made pertinent suggestions, some of which I have incorporated in the text. In this instance I think it best to quote him. "Indices: when it is stated that indices may be treated as linear measurements, I think this depends on the nature of the significant variation of the measurement in the numerator of the index. -- Is the absolute amount of variation of width in mm. what is important, or is it the percentage variation that is important? If the latter I think an alternative linear measure is fairly convenient and more nearly normal -- the difference between the logarithms of the width and radius, $\log(\text{width}) - \log(\text{radius})$: this is essentially the logarithm of the index." In the example used I feel that it is the absolute width of the band that is most important, thus the simple index yields satisfactory results. When in doubt it might be better to use the method suggested by Mr. Calhoun.]

III. FREQUENCIES

Frequency is quite another kind of measurement from those just discussed -- linear measurements and indices. The basic formulae used to analyze frequencies are different. Generally frequencies are reduced to a statement of percent such as "37.5% of the specimens examined show spot 'A'". This really is a very tricky statement, in spite of all of its forthright simplicity. Actually it means very little unless it is accompanied by a statement of the number of specimens involved. A little thought shows that the smallest number of specimens that might be involved is 8 and that in this case 3 of them show spot A. Now it is interesting to know that three specimens before the author bore spot A. But is that really what we want to know? Don't we want to know the frequencies for A that might occur in other samples from the same population? I think it is. There is a simple arithmetic way of determining this.

Because a percent, or frequency, is a single experience based upon a number of specimens, we need know the standard deviation of the observed frequency. The Point Binomial Theorem is used to tell us this S.D. The formula involved is this:

$$\sigma = \sqrt{npq}$$

In this formula "n" is the number of specimens involved, "p" the decimal frequency with which the spot occurs, and "q" the decimal frequency with

* When "p" is very large or very small the S.D. determined by the method outlined does not behave as it is expected to. This is because the curve formed by plotting many "p"s determined from the same population is not a Normal Curve but a skewed curve with quite different mathematical properties.

which the spot is absent ($q = 100 - p$). All you need to do is multiply these three numbers and then take the square root of the final product. That is the S.D. GIVEN IN INDIVIDUALS. To make it applicable to the frequency just convert the number to percent of "n". Now let us go through these steps with our sample of 8 specimens of which three bear spot A.

$$\begin{aligned}\sigma &= \sqrt{8 \times 0.375 \times 0.625} \\ &= \sqrt{8 \times 0.234375} \\ &= \sqrt{1.865000} \\ \sigma &= 1.368 \\ \text{S.D.} &= \frac{1.368}{8} \\ &= 0.171 \text{ or } 17.1\%\end{aligned}$$

Now the bald statement 37.5% becomes 37.5±17.1%. That is quite different, for it means that actually about two-thirds of the time the frequency lies somewhere between 20% and 55%!

To show how great the effect of small sample size is upon the S.D. of a frequency I have calculated this statistic for 37.5 percent frequency using several sizes of samples.

TABLE 6.

The Standard Deviation and certain limits
for 37.5% Frequency

N	S.D.	95% limits	99% limits
8	17.1%	4.2-70.8%	0-81.6%
16	12.1%	13.8-61.2%	6.4-68.6%
64	6.1%	25.6-49.4%	21.4-53.2%
200	3.4%	30.8-44.2%	28.7-46.3%
1000	1.5%	34.5-40.5%	33.5-41.5%

First let me show how to read this table: taking the case of the original sample of 8 specimens it says that 95% or 19 out of 20 samples of 8 specimens each drawn from the same general population as the first sample will have frequencies for spot A anywhere between 4.2% and 70.8% (for practical purposes 0 and 75%); and that 99 out of 100 samples of 8 specimens each drawn from the same general population as the first sample will show frequencies between 0 and 81.6% for spot A (for practical purposes 0 and 75%).

The parenthetical statements "for practical purposes" may bother some. When 8 specimens are involved the frequencies can be only these - 0, 12½, 25,

A skewed curve is crowded to one end, thus S.D. is warped and the 2.5% and 0.5% cut-offs for the 95% and 99% limits are not the same distance each side of "p". Under such conditions Fisher and Yates' Tables (no. VIII) should be consulted.

Brown: SIMPLE STATISTICS FOR THE TAXONOMIST - cont.

37 $\frac{1}{2}$, 50 62 $\frac{1}{2}$, 75, 87 $\frac{1}{2}$, 100 percents. So for practical purposes we take the nearest possible percent to the mathematically determined limits.

This explains my point that "37.5%" standing alone means very little. The point that I want to make is this: A percent frequency standing alone tells you something about the sample being studied but it does not tell you anything about other similar samples from the same population. It lacks prediction value and therefore is of little scientific significance.

It is essential to remember this: When making a statement of percent always state the number of specimens involved or, better still, accompany the percent with its standard deviation.

There are other questions about frequencies that come up such as when two samples are involved that may represent two different populations. Turning again to Mr. Comstock's data on H. charitonius I find that of 100 females from Florida the yellow bands on 44 are washed with rusty scales. Just across the narrow straits lies Cuba. The sample of 46 females from there contains 4 individuals with rusty scales on the yellow bands. The question is this: Do the Florida females differ significantly from the Cuban females in respect to the presence or absence of rusty scales on the yellow bands? Here is how the problem is treated to arrive at a "t"

score. The frequencies are calculated as percent of specimens bearing the rusty scales - 44.0% for the Florida sample and 8.7% for the Cuban. The S.D.s are computed using the point-binomial formula given above -- 5.0% for the Florida sample and 4.2% for the Cuban. The difference in the percent frequencies is found (44.0 - 8.7) to be 35.3%. The S.D. of this difference is found by the same method as used for determining the probable error of a difference (see first article) -- the square root of the sum of the squares of the two standard deviations.

When the above arithmetic has been completed we have the difference in frequencies being $35.3 \pm 6.5\%$. The difference is about 5.4 times the size of its standard deviation. Tables of probability tell us that the odds of observing such a difference in the same population are about 1 in 2 million! I think that I am willing to accept this chance and say that the two populations are really different in this character. CAUTION: When using probability tables for differences in frequency, we are dealing with standard deviations, not probable errors, so we must enter the proper table! Any "t" score above 4.7 for frequencies is as significant as one of 7 for linear measurements when the systems for calculating the "t" score outlined in this series of articles is used.

[To be continued]



The entire September issue of the Journal of the New York Entomological Society is devoted to publication of the "Entomological Reminiscences of William Henry Edwards", with an introduction and annotations by Cyril F. dos Passos. The editor of the Journal has transmitted a note explaining that "the Reminiscences are devoted mostly to Edwards' experiences with Lepidoptera and the publication of the Butterflies of North America, and cover the period from about 1843 to 1902. A number of the collectors and lepidopterists of his day are mentioned and some details concerning them are given." Mr. dos Passos has added many new biographical notes resulting from his research. [See his account in the Lep. News, vol.3: pp.61-62; 1949.] Having had a glimpse of the "Reminiscences", which arrived just as this issue was going to the printer, I can recommend them highly as fascinating and historically important. Non-subscribers to the Journal may purchase them for \$1.50 from:

Mr. Arthur Roensch, Treasurer
N.Y. Entomological Society
American Museum of Natural History
New York 24, N.Y.

Mr. dos Passos has also assembled Edwards' autobiography but has not yet succeeded in finding a publisher.

C.L. Remington



Supplies of additional reprints have recently been sent the News editor for gratis distribution to Society members. They are as follows:

- Evans, W.H., "Life History Notes on Incita aurantiaca Hy.Edw." (1950)
- Field, W.D., "Notes on Erora laeta (Edwards) and Erora quaderna (Hewitson)." (1941)
- Field, W.D., "The Correct Name for the North American Butterfly Variously Called Nymphidia, Calpehelia, or Lehelicca." (1948)
- Field, W.D., "The International Commission on Zoological Nomenclature and the Correct Name for the North American Monarch Butterfly." (1950)
- Field, Clarke, and Franclemont, "On a Recent Proposal to Correct an Error Committed by the International Commission on Zoological Nomenclature at the Paris 1948 Meeting." (1951)
- Leech, H.B., "Flights of Nymphalis californica Bdv. in British Columbia and Alberta in 1945." (1946)
- Leech, H.B., "The Occurrence of a Hollyhock-Seed Eater, Noctuella rufofascialis, at Vernon, B.C." (1949)
- McElvare, R.R., "A New Grotella from S.W. Texas." (1950)
- McElvare, R.R., "Notes on Heliothinae - More Recent Records of Rare Species." (1950)
- Rawson, G.W. and S.A. Hessel, "The Life History of Strymon cecropis Fab. in New Jersey." (1951)

Reprints are postpaid to members outside the U.S.A. Members in the U.S.A. please send postage.



Since its inception, the "Recent Literature on Lepidoptera" section of the Lep. News has included adverse comments on papers being abstracted which have been exceptionally remiss in presenting the essentials which taxonomists almost uniformly agree are necessary when new entities are being named. On just two occasions the "injured" authors have replied to us, attempting in most unconvincing phrases to defend their papers. One of the two, a worker whom we regard as the worst offender in present-day papers on Lepidoptera, wrote very recently, and it occurs to me that it would be well now to set forth my views on several points relating to good descriptions. These views are of course not exclusively or originally my own but for the most part are shared by nearly all modern animal taxonomists.

1. In the description of every new subspecies, species, genus, or other taxonomic entity there must be a clear statement of the CHARACTERS BY WHICH THE NEW ENTITY DIFFERS FROM ITS NEAREST RELATIVE. The practice of giving a lengthy description of part after part (or worse, a skimpy one), with no mention of differences, makes it appear that the author has not made the expected comparisons and therefore is premature or grossly negligent in naming a new entity. The International Rules of Zoological Nomenclature have tried to regulate this point, [Règles, Art.25] but with only mild success.

2. In research with Lepidoptera today, no proposal of a new species can be regarded as complete without a DESCRIPTION OR FIGURE OF THE MALE GENITALIA. It is true that a few cases are on record in which two apparently distinct species are said to show no genitalic differences (scores of such cases have fallen by the wayside when more careful studies were made later, either of the genitalia or of the specific status of the two entities), but genitalic characters of importance are so nearly always present that an adequate describer is obliged to search for them and report on his search. The internal female genitalia have also been used with great success in a few studies, but so little is in print as a basis for comparison, and techniques of preparation are so difficult, that a description of the female genitalia cannot yet be regarded as necessary.

3. Unless financial considerations make figures impossible, EVERY PROPOSAL OF NEW SPECIES SHOULD BE ILLUSTRATED. For Lepidoptera, photographs of wing patterns are usually valuable, especially for subspecies. But perhaps most important are line drawings or excellent photographs of critical structures, such as the genitalia, the venation, the antennae, the palpi, the tarsal claws, and so on.

4. Every author naming a new species or subspecies (race) must give a CLEAR DESIGNATION OF TYPES. At least THE TYPE (holotype) must be designated, and a special label (preferably on red paper) so stating should be attached to the specimen. Many taxonomists also designate one allotype (the sex opposite that of the holotype) and one or more paratypes. Paratypes should, however, be from the same population as THE TYPE; specimens from "more than 50 miles away" or from very different environments should be listed but not designated as paratypes. Cotypes are now archaic and cumbersome, since a later author or

paper must select one lectotype (lectoholotype) from the cotypes. No type should be designated in print unless each specimen listed receives a type label, and of course no specimen can be positively called a type unless it has been so mentioned in the original paper. "Neotypes" have no standing under the Rules to date, and many existing "neotypes" were so loosely chosen that they should be withdrawn. A designator of a neotype should be reasonably sure that the specimen before him represents the same population as had the original type which is now destroyed or lost. [See Lep. News, vol.2: p.26 and vol.3: p.14, for type nomenclature and definitions.]

5. THE FULL DATA OF THE HOLOTYPE MUST BE GIVEN, since the "type locality" is thereby designated. With the growing emphasis on geographic subspeciation and on the population concept, it is probably as important to know the precise "type locality" (the locality in which the population represented by the holotype may be sampled by other workers), as it is to know the characteristics of the type specimen. In well-settled regions with permanent political subdivisions, the nearest town and its county (or equivalent) and province or state should be given. In thinly settled regions a village should be mentioned if possible, but the precise latitude and longitude should also be stated. Specimens collected in mountainous regions should be accompanied by an estimate of the altitude. Obviously, many old specimens and a few recently collected ones have only scanty data, such as "California", "Brasil", etc. In such rare cases, of course the describer is forced to omit a more precise locality. But the author should never publish less than the full data accompanying the specimen designated as holotype.

6. THE DISPOSITION OF THE TYPE MUST BE GIVEN. Furthermore, taxonomists frown more and more on the practice of a private individual retaining the holotype in his own collection. I have noticed that the most enlightened private taxonomists usually present at least the holotype to a museum or other institution with facilities for protecting types and preferably with a permanent staff member responsible for care of the insect collection. Nevertheless, if the holotype is (regrettably) kept in a private collection, that should be so stated. In these days of possible destructive war, it is wise to send a pair of good paratypes to each of several institutions well separated from each other geographically.

7. Every genus named as new should be clearly tied by unequivocal designation to a TYPE SPECIES (generotype, not "genotype"). It is of course desirable to list in addition all the other species which are to be placed in the new genus.

8. A new name (nomen novum) proposed to replace a junior homonym should be clearly marked "nom.nov." or "n.n.", etc. and should never be marked "sp.n." or "gen.nov.", etc.

If there are lepidopterists who wish to take issue with any of these points or to augment them, space will be found in the Lep. News in which their views may be presented.

C.L. Remington

RECENT LITERATURE ON LEPIDOPTERA

Under this heading are listed each month papers on Lepidoptera from all the scientific journals which are accessible to us and our cooperating abstractors. It is hoped that eventually our coverage of the world literature will be virtually complete. It is intended that every paper published since 31 December 1946 will be included. In the first four volumes of the Lep. News 1437 were listed. Abstracts give all new subspecies and higher categories with generotypes and type localities. Papers of only local interest are merely listed. Papers devoted entirely to economic aspects will be omitted. Reprints are solicited from all publishing members and the many regularly received are gratefully acknowledged. Initials of cooperating abstractors are as follows: [P.B.] - P.F. Bellinger; [A.D.] - A. Diakonoff; [L.G.] - L.A. Gozmány; [G.d.L.] - G. de Lattin; [C.R.] - C.L. Remington; [T.S.] - T. Shirōzu. A complete set of these pages, for clipping and filing, may be obtained for Vol.4 for \$0.50, and a subscription for Vol.5 for \$0.50.

40. Avinoff, A., and Walter R. Sweadner, "The Karanasa butterflies; a study in evolution." Ann. Carnegie Mus., vol.32: pp.1-250, 18 pls., 20 figs. 10 Feb. 1951. Revision of this central Asian genus (or subgenus) of Satyridae. Describes as new: K. volgti nigrocellata (Puistagoli, Koh-I-Baba, Afghanistan); K. bolorica hodia (Chodja Mahomet, Afghanistan); K. decolorata grumi (Visharvi Pass, Darwas, Bokhara); K. d. mushketovi (Muzkulak, central Pamir); K. d. roborovskvi (Koshalayak Glacier, W. Pamir); K. d. maureri (Bukhara); K. d. iskander (Hasret Sultan, Bukhara); K. d. maidana (Archi-Maidan, Zaravshan Mts., Russian Turkestan); K. j. josephi hissariensis (Hissar, Bukhara); K. j. darvasica (Visharvi Pass, Darwas, Bukhara); K. j. oshanini (Katelmysh Glacier, Pamir); K. j. angrena (Tschotkal Mts., near Angren, Russian Turkestan); K. j. arasana (Arasas-Bulak, Russian Turkestan); K. j. praestans (Aulie Ata, Syr Daria, Russian Turkestan); K. j. kasak (Targaisk, Kandyktau, Kazakstan); K. wilkinsi robusta (Taldyk Pass, Alai Mts.); K. w. durana (Dura Pass, S. of L. Issyk-kul); K. kirgizorum (Alexander Mts., Russian Turkestan); K. leechi erubescens (Gursy Tash, Pamir); K. l. jacobsoni (Kaindy, Pamir); K. l. alitchura (Alitchur, Pamir); K. l. centralis (Pamir Post); K. l. gregorii (Beik Pass, Chinese Turkestan); K. l. mihmana (Mihman-yuli, Pamir); K. l. hunza (Misgah Hunza, Hindu Kush); K. latifasciata obscurior (Turgen Pass, Russian Turkestan); K. l. occidentalis (Naryn, Russian Turkestan); K. regeli ruckbelli (Burkhan, N. of Djarkent, USSR); K. r. aksuensis (Aksu, Chinese Turkestan); K. r. eburnea (Utchianunak, Kashgar); K. abramovi naryna (Naryn, Russian Turkestan); K. a. lactaea (Yagatch-art, Russian Turkestan); K. pamira ornata (Gursy Tash, Pamir); K. p. holbecki (Gushkon Pass, Darwas, Bukhara); K. p. kafir (Nuksan Pass, Hindu Kush, Kafiristan); K. p. haslundii (Marak, Koh-I-Baba, Afghanistan); K. moorei haarlovi (Kotal Pass, Koh-I-Baba, Afghanistan); K. m. dubia (Baroghil Pass, Chitral); K. modesta gemina (Bara Lacha Pass, Lahoul); K. m. baltorensis (Baltoro Mt., Shigar, Baltistan); K. astorica expressa (Bura Deosai, Ladak); K. rohtanga (Rohtang Pass, India). Gives original description (in English) of all forms of the genus. Figures adults of all forms (usually several specimens; colored figures of most) and ♂ genitalia of most. Pattern and structure of the genus are thoroughly described. The authors prefer to avoid specifying the rank of the various forms, though a formal classification is given for convenience. The genus is extremely intricate, with intergrading 'species' and sympatric 'subspecies'. The grouping of the forms is based on the ♂ genitalia, pattern, and presence and form of androconia. Evolution, dispersal and relationships are discussed and illustrated diagrammatically. [P.B.]
41. Box, Harold E., "Report upon specimens of Diatraea Guilding (Lepidoptera, Pyralidae) in the Cornell University collection." Journ. N. Y. Ent. Soc., vol.58: pp.241-245. 'Dec. 1950' [19 Feb. 1951]. Records of 14 spp. from North and South America. [P.B.]
42. Bretherton, R. F., "Butterflies near Stockholm." Ent. Rec., vol.62: pp.79-80. Sept. 1950.
43. Brower, Auburn E., "Methods for collecting underwing moths (Catocala)" Lep. News, vol.1: pp.19-20. June 1947.
44. Brown, F. Martin, "Colorado Plebeius saepiolus." Ann. Ent. Soc. Amer., vol.44: pp.286-292. July 1951. Describes as new P. g. whymeri (Rampart Range Road, Teller Co., Colo.). Analyzes size and color differences in 6 ssp. of saepiolus, and presents a theory of the origin and dispersal of the species. [P.B.]
45. Corbet, A. Steven, "Proposed use of the plenary powers to suppress the trivial name ajax Linnaeus, 1758 (as published in the binomial combination Papilio ajax) commonly but incorrectly applied to the species named Papilio marcellus by Cramer in 1777 (Class Insecta, Order Lepidoptera)." Bull. Zool. Nomenclature, vol.2: pp.26-29. 20 Apr. 1951. The application of this name to the American P. marcellus or P. polyxenes is invalid. It properly refers to the Oriental P. xuthus, over which name it has priority; but in view of the past confusion regarding the identity of ajax it is recommended that the name be suppressed entirely. [P.B.]
46. Doets, C., "Biology and Variation of Eidophasia messingiella F.R. (Lep., Plutellidae)." Ent. Berichten, vol.12: pp.85-86, 6 figs. 1 June 1950. Attaches new names to four aberrations of wing markings. (In our opinion this procedure is objectionable). [A.D.]
47. Ehrlich, Paul R., and Nicholas W. Gillham, "A New Atrytone from Nebraska (Lepidoptera: Hesperioidea)." Ent. News, vol.62: pp.188-189. June 1951. Describes as new A. conspicua buchholzi (Valley, Neb.). [P.B.]
48. Evans, W. H., "A Catalogue of the Hesperidae from Europe, Asia and Australia in the British Museum (Natural History)." 502 pp., 52 pls., 6 figs. London: British Museum (Natural History), 1949. A running key to subfamilies, genera, species and subspecies, including all 1641 forms found in this area. The key structural characters are described and illustrated in and introductory glossary. Describes as new: BCRBO (type Hesperia borbonica); Bibasid oedipodea paltra (Mindanao); B. miracula (Kuantun, Fukien, China); Allora doleschallii solon (Aola, Guadalcanar); A. major lectra (Biak); A. m. talesia (Talesia, New Britain); Haasora proxissima takwa (Utakwa R., Dutch New Guinea); H. anura china (Ta Tsien Lou, China); H. danda (Kalaw, S. Shan States); H. discolor eira (New Ireland); H. borneensis luza (Leponto, N. Luzon); H. taminatus andamana (S. Andamans); H. hurama mola (Batchian, Malay Archipelago); H. schoenherri gaspa (Naga Hills); H. vitta manda (S. Andamans); H. khoda plexa (Buru); H. leucospila spila (Amboina); Chaetocneme calligenus stringa (Hydrographer Mts., Br. New Guinea); Capila phanaeus fiducia (Khasi Hills, Assam); C. p. falta (Kanbauk, Tavoy); Lobocla lilliana gesta (Momeit, N. Burma); L. l. tonka (Ngai Tio, Tonkin); Celaenorrhinus oscula (Tien Tsuen, China); C. ratna daphne (Kumaon, India); C. morena (Naga Hills); C. putra questa (Liwa, Sumatra); C. munda ioka (Tsekou, Yunnan); C. dhanada hanna (Kanbauk, Tavoy); C. d. herga (Sumatra); Darpa

48. Evans (cont.)

striata minta (Sebong, Manipur); *Coladenia dan festa* (Kirbari, Naga Hills); *C. d. fatua* (Gangtok, Sikkim); *C. d. fabia* (Margherita, Assam); *C. laxmi landa* (Sebong, Manipur); *Saranessa purendra pandra* (Karwar, N. Kanara); *S. dasahara adona* (Pachmarhi); *S. d. sandra* (Middle Andaman Is.); *Seseria dohertyi scon* (Lou Tse Kiang, Yunnan); *S. d. salex* (Hainan); *S. sesame* (Sarawak); *Pintara pinwilli banga* (Tameang Lajang, Borneo); *Daimio tethys roona* (Se-Pin-Lou-Chan, Ya-Tcheou, China); *D. phisara rex* (Tse Kou, Tibet); *Tagiades parra gala* (Sikkim); *T. p. naxos* (Perak); *T. waterstradti talanga* (Gunong Talang, Pad Bovenland, Sumatra); *T. nepaka landa* (Lebong Tandai, Mt. Lalangia, Sumatra); *T. trebellius lola* (Treasury Is.); *T. nestus juncta* (Obi, Moluccas); *T. p. brunta* (Woodlark Is.); *Abraximorpha davidii esta* (Ngai Tio, Tonkin); *A. d. eifina* (Java); *Odontoptilum angulata sinka* (Los Baños, Luzon); *Caprona agama subina* (Sumba, Sunda Is.); *C. a. alora* (Alor Is., Dutch New Guinea); *C. alida vespa* (Nilgiris); *C. a. verburyi* (Kootur, Chittar Pahar, Punjab); *Ervnis montanus monta* (Tse Kou, Yunnan); *E. marloyi max* (Khojak, Baluchistan); *E. m. pathan* (Chitral, Utsun Valley, India); *Carcharodus alceae gooraisa* (Goorais, Kashmir); *Spialia osthelderi gecko* (Hyrcania, Persia); *S. doris daphne* (Ziz Valley, Atlas Mts.); *Muschampia tessellum targa* (Ordub, Persia); *M. proto lambesa* (Lambese, Algeria); *M. poggei patta* (Kuliab, Afghanistan); *M. staudingeri musta* (Paghman Mts., Afghanistan); *M. g. loga* (Logar Valley, Afghanistan); *M. g. phil* (Chotair, Baluchistan); *Felicena dirpha nota* (Goodenough Is.); *F. dora* (Majoebui, New Guinea); *Toxidie incornatus anga* (Angabunga R., Br. New Guinea); *Carterocephalus houangty bootia* (Gyatsa, Bhutan); *Baracus vittatus gotha* (Animalai Hills); *Ampitia dioscorides singa* (Ceylon); *Aeromachus stigmata shanda* (Kalaw, S. Shan States); *A. ihora creta* (Khasi Hills); *A. j. skola* (Battak Mts., Sumatra); *A. dubius impa* (Imphal, Manipur); *Sovia malta* (Kabru, Manipur); *Pedesta blanchardii shensia* (Tapai Shan, S. Shensi, China); *P. bajleyi nanka* (Wushi, Szechwan); *Thoresa fusca strona* (Kuantun, Fukien); *Halpe homolea molta* (Sikkim); *H. h. filda* (Mangpo, Sikkim); *H. h. banda* (Thandaung, Karen Hills, Burma); *H. dante dante* (Negros); *H. d. luzona* (Palali, Benguet, Luzon); *H. d. tilia* (Mindanao); *Eogenes alcides uraka* (Urak, Baluchistan); *E. g. chitrala* (Chitral); *Koruthalaloe rubecula cachara* (Cachar Rd., Manipur); *K. r. rubina* (Kina Balu, Borneo); *K. r. yerona* (Java); *K. r. balina* (Bali); *K. r. ponta* (Palawan); *K. r. atra* (Mindanao); *K. sindu monda* (Naga Hills); *K. g. tanga* (Nias); *K. focula frena* (Kina Balu, Borneo); *Stimula swinhoi disca* (Karen Hills, Burma); *Ancistroides gemmifer dorna* (Sipora Is.); *Notocrypta paralygos mangla* (N. Kanara, India); *N. p. teuta* (Nias); *N. clavata theba* (E. Dawnas, Burma); *N. curvifascia corinda* (N. Korintji Valley, S. W. Sumatra); *N. renardi roona* (Roon Is.); *N. walgensis wanga* (25 mi. from Wangar, Nomnagihé, Dutch New Guinea); *N. maria* (Owgarra, Br. New Guinea); *Scobura cephaloides kinka* (Tonkin); *Suada swerger suava* (King Is., Mergui); *S. g. sedata* (Liwa, Sumatra); *Hyarotis microstictum coorga* (Sati R., Coorg, India); *Isma obscura fonta* (Sumatra); *I. g. vulsina* (Mt. Gedé, Java); *Plastinia mangola* (Sula Mangola); *P. tessellata tessa* (Sangir Is.); *Lotongus calathus balta* (Kanbauk, Tavoy); *Gangara thvraia pandina* (Java); *Matapa cresta* (Sikkim); *Unkana ambasa tranga* (Nias); *Hidari doesoena gloria* (Kina Balu, Borneo); *Acerbas anthea pista* (Hoop Bon, Siam); *A. duris dorka* (Pulo Laut, Borneo); *A. gelta* (Lawas, Borneo); *Pirdana distanti spenda* (Kawke-reik, Dawnas, Burma); *Cyrina cyrina corpa* (Borneo); *Prada rawlinsonia* (Rawlinson Mts., New Guinea); *Thymelicus actaeon orana* (Algeria); *T. leonina tatsia* (Ta Tsien Lou, China); *Hesperia comma shandura* (Shandur

Pass, Chitral); *Ochloides subhyalina pasca* (Khasi Hills, Assam); *O. thibetana sanku* (Htawgaw, Burma); *O. siva targa* (Pochu Valley, S. E. Tibet); *Taractrocera ziclea bessa* (Toekan Bessi, Dutch E. Indies); *Ocybadistes flavovittata kokoda* (Kokoda, New Guinea); *Oriens fons* (Los Baños, Luzon); *Potanthus omaha bione* (Mindanao); *P. taxilus rabida* (Batjan); *P. mara kansa* (Kwei Chow, China); *P. ganda marla* (Borneo); *Telicota doba* (Dobo, Aru Is.); *T. colon stinga* (Malacca); *T. c. vega* (New Ireland); *T. g. gara* (St. Mathias Is.); *T. augias florina* (S. Flores); *T. linna linna* (Sikkim); *T. l. besta* (Hainan); *T. l. bina* (Sumatra); *T. l. bac-tra* (Java); *T. l. bodra* (Borneo); *T. ancilla volens* (Timor); *T. g. baudina* (Baudin Is., N. Australia); *T. a. mamba* (Biagi, Mambare R., New Guinea); *T. vinta* (Kapeur, Dutch New Guinea); *T. ohara iix* (Sikkim); *T. o. vedanga* (Java); *T. o. iactus* (Kina Balu, Borneo); *T. o. iania* (Mindanao); *T. o. iona* (Kezeli, Buru); *T. o. ixion* (Upper Aroa R., New Guinea); *T. kezia kezia* (Mt. Mado, Buru); *T. k. lenna* (Talesoa, New Britain); *T. ternatensis ranga* (Sangir, Dutch E. Indies); *T. t. sula* (Sula Mangoli); *T. t. aruba* (Aru Is.); *T. t. solva* (Florida Is., Solomons); *T. t. fenia* (Feni, New Ireland); *T. sadra* (New Guinea); *T. gervasa* (Duke of York Is.); *Cephrenes agiades tugela* (Tugela Is., Solomons); *Pastria pastria* (Mambare R., Br. New Guinea); *Banta banta* (Angabunga affluent, St. Joseph R., Hydrographer Mts., Br. New Guinea); *Kobrona denva* (Edie Creek, Central New Guinea); *K. pansa panta* (Edie Creek, Central New Guinea); *K. edina* (Edie Creek, Central New Guinea); *K. vanda* (Edie Creek, Central New Guinea); *K. croma* (Zegeheme, Cromwell Mts., New Guinea); *K. idea* (2 days N. of Fak-Fak, Dutch New Guinea); *Sabera fuliginosa chota* (Biagi, Mambare R., New Guinea); *S. bicolor misola* (Misol); *S. kumpia kumpia* (Mt. Kumpi, Menoo R., Weylandt Mts., New Guinea); *S. k. baxta* (Biagi, Mambare R., New Guinea); *S. biaga* (Biagi, Mambare R., New Guinea); *S. aruana lina* (Mt. Lina, Cyclops Mts., Dutch New Guinea); *S. dobboe handva* (New Hanover); *Mimene biakensis gunta* (German New Guinea); *Parnara guttatus batia* (Kuatuni, Fukien); *P. g. andra* (Matang Rd., Borneo); *Pelopidas agna dingo* (head of Aroa R., New Guinea); *P. thrax masta* (Imphal, Manipur); *Polytremis pellucida quanta* (Kwangtseh, Fukien). Considerable revision has been done; e.g. *Eughemon* is included in a group of genera in the Pyrginae. The polytypic species concept is adopted; related forms which represent each other geographically are treated as subspecies. The location of each holotype is given. There is a bibliography and list of accessions, and a list of spp. not determined or found to be extralimital. 132 previously unfigured spp. and ssp. are illustrated in color. The ♂ genitalia of all but 2 spp; and of many ssp. are figured. [P.B.]

49. Ferreira d'Almeida, R. F., and José Oiticica F., "The International Commission on Zoological Nomenclature and the Name of the Monarch Butterfly." *Science*, vol. 113: pp.728-729. 22 June 1951. Protest against the suggestion by the secretary of the Commission that type and type locality of *Plexippus* be fixed again, to correct an earlier error; in this case, the suggested type specimen still does not come from the type locality! [P.B.]

50. Field, William D., J. F. Gates Clarke, and J. G. Franclemont, "On a Recent Proposal to Correct an Error Committed By the International Commission on Zoological Nomenclature at the Paris 1948 Meeting." *Science*, vol. 113: pp.68-70. 19 Jan. 1951. Discussion of Hemming's attempt to settle the application of "*Danaus plexippus*"; the authors give reasons for the restriction of this name to the Oriental insect ("*geny-tia*") and the use of *menippe* for the Monarch. [P.B.]

RECENT LITERATURE ON LEPIDOPTERA - cont.

51. Franclemont, John G., "A New Generic Name (Lepidoptera, Phalaenidae, Acontiinae)." Proc. Ent. Soc. Wash., vol.52: pp.271-272. 25 Oct. 1950. Proposes THIOPTERA to replace Xanthoptera, a homonym. [P.B.]
52. Franclemont, John G., "Notes on Some Genera and Species of Eastern Moths with Descriptions of New Species (Lepidoptera, Phalaenidae)." Bull. Brooklyn Ent. Soc., vol.45: pp.144-155, 9 figs. Dec. 1950. Describes as new: Procus crytora (New Brighton, Pennsylvania); Zale phaeocapna (New Brighton, Pennsylvania); Figures genitalia of both and of P. semicana. The following name changes must be made: Procus for Oligia; Meropleon for "Oligia" diversicolor and ambifusca; Apamea for Septis; A. amputatrix for "S." arctica; Amphipoea for Apamea; Zenobia for Ipipomorpha; SUNIRA for Rusina circellaris and North American spp.; Unca for Erastria and Lithacodia; Zale lunifera for Z. cingulifera; Z. lineosa for Z. lunifera; Cae-nurgia chloropha for C. convallescens. [P.B.]
53. Franclemont, John G., "The Species of the Leucania unipuncta group, with a Discussion of the Generic Names for the Various Segregates of Leucania in North America (Lepidoptera, Phalaenidae, Hadeninae)." Proc. Ent. Soc. Wash., vol.53: pp.87-85, 11 pls. Apr. 1951. Describes as new: PSEUDALETIA (type Leucania unipuncta Haworth); P. unipuncta quechua (Incachaca, Cochabamba, Bolivia); P. cunyvada (Bogotá, Colombia); P. roraimae (Mt. Roraima, Brazil); P. sequax (Jalapa, Mexico); P. australis (Port Victor, South Australia); P. idisana (Baguio, Luzon, Philippines). New genus also includes 'Leucania' antica (unipuncta ssp.), adultera, punctulata and separata. Reviews all generic names applied to the Leucania group of genera. Presents a revised checklist of North American spp., divided on the basis of ♂ genitalia among Faronta (= Protoleucania), with aleada, tetra, diffusa, rubripennis and quadrannulata; Pseudaletia; Aletia, with oxygala and yukonesis; and Leucania (remaining spp.). Figures ♂ and ♀ genitalia of all entities in Pseudaletia, and of 10 representatives of related genera. [P.B.]
54. Hardwick, D. F., "Preparation of Slide Mounts of Lepidopterous Genitalia." Canad. Ent., vol.82: pp. 231-235. Nov. 1950. Comprehensive directions; applicable mainly to Macrolepidoptera. [P.B.]
55. Hemming, Francis, "On the proposal that the trivial name ajax Linnaeus, 1758 (as published in the binominal combination Papilio ajax) should be suppressed by the International Commission on Zoological Nomenclature under its plenary powers." Bull. Zool. Nomenclature, vol.2: pp.29-30. 20 Apr. 1951. See Corbet, no. 45 above. Suggests alternatively that ajax be affixed to "the Nearctic species to which it is now usually applied" but does not state whether marcellus or polyxenes would be supplanted. [P.B.]
56. Herbulot, C., "On the Presence of Middle Spurs in the Hind Tibiae of a Male Scopula (Lep. Geometridae)." Entomologist, vol.83: p.225. Nov. 1950.
57. Hinton, H. E., "Myrmecophilous Lycaenidae and Other Lepidoptera - a Summary." Proc. Trans. South London Ent. Nat. Hist. Soc., 1949-50: pp.111-175, 9 figs. Apr. 1951. Following a discussion of theoretical considerations, and descriptions of larval and pupal organs of importance in the ant-lycaenid relationship, the author summarizes all known life histories of myrmecophilous Lycaenidae, plus those of predaceous forms and those which feed upon secretions of other insects, plus what little (relatively) is known about myrmecophily in other families of Lepidoptera. There is a bibliography of all important papers on the subject up to 1947, and an index to spp. of Lepidoptera and ants mentioned. A fascinating and invaluable paper. [P.B.]
58. Hoffmeyer, Skat, "Problems in Danish Macrolepidoptera." Entomologist, vol.83: pp.193-198. Sept. 1950.
59. Huggins, H. C., "Sterrhia muricata Hufnagel in England." Entomologist, vol.83: pp.234-235. Oct. 1950.
60. Hyde, George E., "A Gynandrous Agrotis puta Hübner." Entomologist, vol.84: pp.23-24. Jan. 1951.
61. Kiriakoff, S. G., "Recherches sur les organes tympaniques des Lépidoptères en rapport avec la classification. VI. Nyctemeridae" [In French]. Bull. Ann. Soc. Ent. Belg., vol.87: pp.106-129. 5 July 1951. Considers the following groups, usually placed as subfamilies of the Arctiidae, as tribes in the family Nyctemeridae: PERICOPIINI (with subtribes AGANEIDES (= 'Hypsidae') and PERICOPIDES), CALLIMORPHINI, and NYCTEMERINI. Discusses classification and phylogeny, basing his conclusions on a study of the tympanum of representatives of 33 genera. [P.B.]
62. de Lesse, H., "Expeditions polaires françaises (Missions Paul-Émile Victor). Zoologie. - 4^e note. Macrolepidoptera" [In French]. Ann. Soc. Ent. France, vol.118: pp.54-78, 38 figs. 1951. Describes as new Operophtera groenlandica. Extensive notes on the 19 spp. collected on the northwest coast of Greenland, belonging to the Pyralidae, Geometridae, Phalaenidae, Lymantridae, Nymphalidae and Pieridae. Figures ♂ and ♀ genitalia of almost all spp., and setal pattern of O. groenlandica larva. [P.B.]
63. de Luca, C., "A contribution to the list of Maltese Lepidoptera." Ent. Mo. Mag., vol.86: pp.232-233. Aug. 1950. 25 new records. [P.B.]
64. de Luca, C., "Additional Records of Micro-Lepidoptera of the Maltese Islands (Heterocera)." Entomologist, vol.83: pp.249-251. Nov. 1950. 14 new records. [P.B.]
65. McDonald, Howard, "Biology and Control of Heliothis ononis Schiff., an Important New Pest of Flax in Western Canada." Ohio State U. Agr. Doct. Diss., no.53: pp.231-240, 5 figs. 1947.
66. McDunnough, James H., "On the Identity of Agrotis pyrophiloides Harvey (Lepidoptera, Agrotinae)." Bull. Brooklyn Ent. Soc., vol.46: pp. 19-20. Feb. 1951. Notes on type and genitalia of this Pronoctua.
67. McElvare, Rowland R., "Note on Chlorocleptria jaegeri." Bull. Brooklyn Ent. Soc., vol.46: p.28. Feb. 1951.
68. McElvare, Rowland R., "Notes on Heliothiinae - more recent records of rare species." Bull. Brooklyn Ent. Soc., vol.46: p.51. Apr. 1951. Records of four spp. from southern United States. [P.B.]
69. Mackay, Margaret R., "Species of Eupithecia reared in the Forest Insect Survey in British Columbia (Lepidoptera: Geometridae)." Canad. Ent., vol.83: pp.77-91, 4 pls. Apr. 1951. Describes as new: E. transcanadata (Fernie, Kootenai Dist., B. C.); E. pseudotsugata (Otter L., Kamloops Dist., B. C.); E. harrisonata (Harrison L., New Westminster Dist., B. C.); E. columbiata holbergata (Holberg Inlet, Vancouver Is.); E. vinsullata (Vinsulla, Kamloops Dist., B. C.); E. kananaskata (Kananaskis, Alberta). Describes the ♀ of E. usurpata. Summarizes the spp. of the filmata group. Adults and genitalia of these spp. are figured. Food plants are recorded for the above and for a number of other spp. [P.B.]
70. Munroe, E. G., "A previously unrecognized species of Nymphula (Lepidoptera, Pyralidae)." Canad. Ent., vol.83: pp.20-23, 1 pl., 2 figs. Jan. 1951. Resurrects N. curviferalis (Walker) from synonymy under N. badiusalis; describes both, figuring adults and ♂ genitalia. [P.B.]

71. Munroe, Eugene G., "The systematics of *Calisto* (Lepidoptera, Satyriinae), with remarks on the evolutionary and zoogeographic significance of the genus." *Journ. N. Y. Ent. Soc.*, vol.58: pp.211-240. 19 Feb. 1951. Describes as new *C. smintheus bradleyi* (Rio Tacoluco, Sierra Range, Pinar del Rio Province, Cuba). Gives characters of genus, and key to spp. and ssp. Lists all known forms, with notes. Discusses distribution and speciation. Genus is confined to the Antilles, with center in Hispaniola, which has the only primitive spp. This distribution may be explained by the size of the island, its relative stability geologically, and its mountainous terrain, which has permitted local subspeciation. The other islands have lost their original fauna in geologic changes. [P.B.]
72. Munroe, Eugene G., "North American Pyraustinae: notes and descriptions (Lepidoptera: Pyralidae)." *Canad. Ent.*, vol.83: pp.161-169, 1 pl., 14 figs. July 1951. Describes as new: *CYLINDRIFRONS* (type *Botis succandialis* Hulst); *Pyrausta perrubralis sanchialis* (Duncan, British Columbia); *Titanio criddlealis* (Aweme, Manitoba); *Noctuella atascaderalis* (Atascadero, Calif.). The following changes are made: *Pionea helvalis*, type of *Framinghamia*; *Spilodes palindialis*, type of *Trischistognatha* (these resurrected genera are redescribed); *Pyrausta unimacula* to *Evergestis*; *Titanio ephippialis* to *Loxostege*; *P. socialis* removed from synonymy; *P. funebris glomeralis* is the distinct North American sp. Discusses 3 ssp. of *P. perrubralis*. Figures adults of new spp. and ssp. and 6 other forms, ♂ genitalia of 12 spp., and heads of 4. [P.B.]
73. Paclt, Jiří. "A new family name in Lepidoptera." *Ent. Berichten*, vol.13: p.219. 1 Feb. 1951. Proposes TETHEIDAE for Palimpsestidae (= Cymatophoridae, Thyatiridae, Polyplocidae); adds a survey of European genera. [A.D.]
74. Rawson, George W., and Sidney A. Hessel, "The life history of *Strymon cecrops* Fabricius (Lepidoptera, Lycaenidae)." *Bull. Brooklyn Ent. Soc.*, vol.46: pp.79-84, 1 pl., 1 fig. June 1951. Describes early stages, with figures of each. Habits of larva and adult are discussed. [P.B.]
75. Rindge, Frederick W., "A change in synonymy in *Drepaulatrix* (Lepidoptera, Geometridae)." *Journ. N. Y. Ent. Soc.*, vol.59: pp.63-64. 25 June 1951. *D. ella* is probably a northern sp. of *D. bifilata*. [P.B.]
76. Silva, Pedrito, "Stenoma decora Zeller (Lep. Stenomatidae), uma nova praga potencial do cacauzeiro na Baía, Brasil" [In Portuguese, English summary]. *Revista Ent.*, vol.17: pp.361-374, 16 figs. 'Dec. 1946' [20 Jan. 1947]. Describes larva, pupa and adults in detail. Food plants *Theobroma leicocarpa*, *Ceiba pentandra*. Discusses systematic position, distribution, and habits. Records 1 parasite. [P.B.]
77. Sperry, John L., "Geometrid notes." *Bull. So. Cal. Acad. Sci.*, vol.50: pp.50-53. 20 Apr. 1951. Describes as new *Chlorochlamys hesperia* (Borrego, California). Revisional notes on *Chlorochlamys*, and notes on three other species. [P.B.]
78. Stampfer, H., "Contribution à l'étude des Lycaenidae de la faune éthiopienne (Lep.)." [In French]. *Bull. Soc. Ent. France*, vol.52: pp.35-41. 20 May 1947. Describes as new: *Anthene livida galla* (Maji, Abyssinia); *A. otacilia benadiensis* (Afko, Italian Somaliland); *A. lachares toroensis* (Bwamba, Toro, W. Uganda); *Neurellipes staudingeri obsoleta* (Kakamega, Kavirondo, Kenya); also two 'forms'. Describes the previously unknown ♂ of *Eresina bilinea* and *E. crola*, and ♀♀ of *Anthene kampala* and *A. katera*. Several additional notes. [P.B.]
79. Tilden, James W., "The insect associates of *Baccharis pilularis* de Candolle." *Microent.*, vol.16: pp. 149-185. 12 Apr. 1951. Lists, among other insects, 23 spp. of Lepidoptera feeding on this plant. *Oncophila v-flavum* is a new American record. Records parasites and feeding habits, and other aspects of the ecology of this community. [P.B.]
80. Turner, A. Jefferis, "Revision of Australian Lepidoptera. Oecophoridae. XIV." *Proc. Linn. Soc. N. S. Wales*, vol.72: pp.143-158. 15 Sept. 1947. Treatment of the 'Depressiades' group. Describes as new: *ANCISTRONEURA*, and type species *A. thaumasia* (Macpherson Range, Queensland; Sidney); *A. ammophara* (Kuranda, N. Queensland); *IDIOCHROA*, *I. anthina* (Nambour, Mt. Tamborine, and Brisbane, Queensland); *Pholeutis appreta* (Macpherson Range, Queensland); *P. leucoprepta* (Macpherson Range, Queensland); *P. acroprepta* (Macpherson Range, Queensland); *LEUROBELA* (type *holophaea* Turn.); *L. clasmita* (Macpherson Range, Queensland); *L. puncta* (Stannary Hills, N. Queensland); *DYSTRENETA*, *D. Lepta* (Kuranda, N. Queensland); *DELOPHANES* (type not specified; *anthracephala* Lower only sp. listed); *Eutorna dysphanes* (Bunya Mts., Queensland); *E. plumbea* (Albany, and Denmark, W. Australia); *MACROBELA*, *M. abrupta* (Perth); *Eupselia beltera* (Charleville, Queensland); *E. axiopaena* (Toowoomba, Queensland); *E. metabola* (Emerald, Dalby, Talwood, and Stanthorpe, Queensland; Adelaide; Perth); *PROGONICA*, *P. niphostibes* (Stanthorpe, Queensland); *BLEPTOCHITON*, *B. leucotrigona* (Eugella, N. Queensland); *Thudaca monoclechia* (Cape York, N. Queensland); *T. rubrilinea* (Cunderdin, W. Australia); *T. coryeropsis* (Maryland, N. S. Wales); *T. litodes* (Emerald, Queensland); *ACRAEPHNES*, and type sp. *A. nivea* (Rockhampton, Emerald, and Stanthorpe, Queensland; Tenterfield and Brunswick Hds., N. S. Wales); *A. nitida* (Warooka, W. Australia); *HAERETA*, and type sp. *H. cryphimaea* (Mt. Tamborine, Queensland); *H. niphosceles* (Lake Barrine, N. Queensland); *H. inscripta* (Ooldea, S. Australia); *BRACHYZANCLA*, and type sp. *B. poenicca* (Bunya Mts., Queensland); *B. sporima* (Stanthorpe, Queensland); *B. acrocossa* (Goodna and Toowoomba, Queensland); *B. dysgenes* (Toowoomba, Queensland); *B. leptodes* (Macpherson Range, Queensland); *B. placophora* (Linsmore, N. S. Wales); *B. baea* (Broken Hill, N. S. Wales); *Peritorneta ligopsis* (Duarina, Jandowae, Injune, and Bollon, Queensland); *Cryptolechia striata* (Brisbane); *C. amaurophanes* (Murrurundi, N. S. Wales); *C. epinephela* (Mt. Tamborine and Macpherson Range, Queensland); *C. irabela* (Kalamunda, W. Australia); *C. brachymita* (Perth); *C. leptosticta* (Cooktown, Kuranda, and Lake Barrine, N. Queensland); *C. inquinata* (Kuranda, N. Queensland). Location of type specimens not always stated; specimens not otherwise mentioned. Type localities not specified; all recorded localities are given above. 31 genera listed, with descriptions, references, and a key to all but *Analcodes* (said to be 'weak'); 143 spp. listed, with references and localities. [P.B.]
81. Wakely, S., "*Eucnaemidophorus* (*Platyptilia*) *rhododactyla* Schiffermüller." *Entomologist*, vol.83: pp.236-237. Oct. 1950. Life history notes. [P.B.]
82. Williams, C.B., "Changes in insect populations in the field in relation to preceding weather conditions." *Proc. Roy. Soc. Lond. B*, vol.138: pp.130-156, 9 figs. 15 Feb. 1951. Changes in total insect population as measured by light-trap captures are closely correlated with rainfall and minimum temperature in the preceding three months. [P.B.]
83. Williamson, Margaret, *The First Book of Bugs*. 45 pp.; ill. Franklin Watts, New York. 1949.
84. Woke, Paul A., "Notes on a migratory flight of *Urania fulgens* Walker (Uranidae) on the Isthmus of Panama, Central America." *Proc. R. Ent. Soc. Lond. (A)*, vol.26: pp.38-39. 16 Mar. 1951. Flight involved millions of individuals and lasted well over a month. [P.B.]

OFFERINGS AND NEEDS OF MEMBERS

Lepidopterists' Society members may use this page free of charge to advertise their offerings and needs in Lepidoptera. The Editors reserve the right to rewrite notices for clarity or reject unsuitable notices. Unless withdrawn sooner by the member, each notice will appear in three numbers. We can not guarantee any notices but expect all to be bona fide. Please notify us of any abuse of this service.

I will pay LEPIDOPTERISTS' SOCIETY DUES for foreign (or N. American) collectors in exchange for shipment of butterflies of equal value, or will pay cash direct. Want butterflies from any tropical island, Africa, and Indo-Australia, Central and South America; NOT Europe at present. Also want North American species in quantity, esp. Papilio. Must be first quality, in papers. Want all families but esp. Nymphalidae, Papilionidae, Morphidae, and Saturniid moths; also other large insects. Will advance money to any good collector. Send list and prices in first letter. A. Glanz, Butterfly World Supply House, 289 E. 98th St., Brooklyn 12, New York.

Japanese Rhopalocera and some moths, including Japanese (and including Formosan) Rhopalocera and some moths offered in exchange for Rhop. and some moths from all parts of the world. Especially Satyridae, Lycaenidae, Papilionidae, Nymphalidae, Pieridae, Saturniidae and Arctiidae. Seiji Ishida, 33 Nakayama-chô, Saga, Ukyô-ku, Kyoto City, JAPAN.

Austrian hunter and collector (not dealer) in Amazon and Matto Grosso districts of Brazil takes orders for Lepidoptera and other insects, all with full locality and date. Also supplies amphibians, reptiles and various terrarium animals. Write (in German if possible) to: Walter A. Riffler, Técnico Zoológico, Caixa Postal 500, Belem, Pará, BRAZIL.

Huge AFRICAN LEPIDOPTERA collection for sale; over 2000 moths and 5400 butterflies. About 250 types, with complete data, all on pins. Will sell in part or complete, including 120 glass cases. Also, rare books on African Lepidoptera. Ari W. Kampf, Franz Jurgens Strasse 12, Dusseldorf, GERMANY.

AUSTRALIAN LEPIDOPTERA for sale, papered or pinned, perfect specimens, with data, 10¢ each. Write stating needs; Victorian species only offered. Ian Harman, c/o Mrs. A.H. Bisdee, Appletree Cottage, Dorset Road, Croydon, Victoria, AUSTRALIA.

Exchange desired in all groups of Macros, esp. Geometridae. Lepidoptera from COLORADO (Parnassius, Colias, Oeneis, etc.), ILLINOIS, and southern INDIA-NA offered in trade. Ronald H. Leuschner, 1172 S. Wenonah Ave., Oak Park, Illinois.

Wanted to buy: SEITZ' "Macrolepidoptera of the World", Vols. 1, 9, 13, English translation. George H. Berg, Rm. 319, Custom House, New Orleans 16, La.

MEGATHYMUS WANTED - specimens of this genus from all localities. Will buy or exchange. Have Megathymus for exchanges. Don B. Stallings, Caldwell, Kansas.

GENITALIC VIALS: On Nov. 1st I shall place an order with Kimble Glass Co. for following sizes of vials:

1. 3-3/4 to 4-1/2 by 10 ± 2 mm.
2. 6-1/4 to 7 by 15 ± 2 mm.
3. 7-1/4 to 8 by 18 ± 2 mm.
4. 1/4 dram; 9 x 30 mm.

Anyone wanting some of these vials should notify me so I can include his order with mine, as these are made on special order. (I will make no extra charge.) Kent H. Wilson, 823 East "B" St., Moscow, Idaho.

MEGATHYMUS YUCCAE ALABAMAE ex-pupae 1951, perfect, spread. Want exotics and Gulf States rarities in exchange.

H.W. Eustis, 2301 Woodbine Rd., Augusta, Georgia.

BUTTERFLIES FROM ARCTIC and Far North especially Oeneis, Erebia, Eoloria, at reasonable prices. R.J. Fitch, 2235 Pandora St., Vancouver, B.C., CANADA.

Wanted: Seitz' "Macrolepidoptera of the World", esp. Vols. 1, 2, 6, 9, 13, English Translation. G.F. Schirmer, 2912 N. 45th St., Milwaukee 10, Wis.

Lepidoptera of the SOUTHWEST U.S.A. for sale, papered or pinned. Lots of 100, either Rhopalocera, Macros, or Micros, priced low, full data.

F.P. Sala, 1764 Colorado Blvd., Los Angeles 41, Cal.

Speyeria diana, S. cybele leto and letona, and S. nokomis nitocris, ♂ and ♀ with full data, offered in exchange for needed species of Erebia and Oeneis, esp. the following numbers from McDunnough 1938 list: 127b-e; 130a-c; 135a; 136a; 138b,c; 140, 143a; 144b-c; 147; 147a; 149b-d; 151, 152. Also need any of forms recently described by dos Passos except taygete fordii and rossii gabrieli. If you have some of these species but are not interested in the Speyeria, send list of desiderata.

Paul R. Ehrlich, 538 Academy St., Maplewood, N.J.

Bio Metal standard redwood insect box, new style, 9 x 13 x 2-1/2 inches. Screw on hinge. \$2.25 each, \$25/doz. Also Cornell drawers and unit pinning trays. Equipment constructed to order. Bio Metal Associates, Box 346, Beverly Hills, Calif.

LIVING MATERIAL

The Editors will welcome especially notices for the exchange or sale of Lepidoptera eggs, larvae, and pupae, hoping to revive the old interest in rearing and to re-emphasize the importance of studying the immature stages. Contributors are urged to include accurate locality data with all material sent.

Wanted to buy: cocoons of U.S.A. Saturniidae, pupae of Sphingidae, Papilio chrysalids, Catocala eggs, Hemileuca maja egg rings. Will exchange best make rust-proof steel pins Nos.0-7, value \$4.00 per thousand, for cocoons and Coleoptera. Eugene Dluhy, 3912 N. Hamilton, Chicago 18, Illinois.

Q. "Do you believe that the Viceroy (Limenitis archippus) mimics the Monarch (Danaus plexippus)? Are there other North American butterflies that mimic protected species?"

A. I believe it is a Müllerian mimic (resemblance between two protected butterflies, to the advantage of both), but that the Monarch is the dominant partner. In Florida and the Southwest other races of the Viceroy mimic the local races of the Queen. I believe also that there is a mimicry group (partly Müllerian, partly Batesian) surrounding the Green Swallowtail (philenor). This includes Papilio troilus, Limenitis astyanax, P. glaucus, and in a degenerate way P. polyxenes. I believe that mimicry is best developed in the tropics, where there are more butterfly-eating birds, and also the monkeys, and that in North America it may be partly a left-over from an earlier geological period when it was much warmer here, and is therefore now degenerating.

In the moths we also have local mimics of Hymenoptera (the Aegeriidae, and perhaps best of all Cis-seps fulvicollis, which in life is a very good mimic of Polistes). Also Lycomorpha pholus is a (perhaps degenerate) mimic of Calopteron beetles; many tropical relatives are effective mimics of Lampyridae.

Q. "In the spreading of Golias and some other species, there is a staining of the hind wings where they come in contact with the body while in the relaxing jar. What can be done to remove this stain?"

A. You do not state what type of stain. Grease, soaking out from the body, can be easily removed by any fat solvent, such as pure gasoline or benzol. I drop papered material in the solvent, leave some hours, blot off and dry; for spread material I prefer to lay out the specimen on an old setting board (a size or two over-size) with pads of cellulocotton below and above the wings and over the body; then soak the whole with benzol or chloroform, cover the wing pads with glass (microscope slides) and leave till dried out. Then remove the pads and the grease will have been drawn out into the pads. If the stain is cyanide (scarlet if not too heavy) there is no remedy; - clean up your cyanide bottle.

W.T.M. Forbes



In reference to the Question and Answer column of the News, vol.4: p.60, it should be noted that Papilio (Menelaides) alcinous Klug feeds on Aristo-lochia in Japan. It is the sole representative of the "Pharmacophagous" group in our country. Dyar remarks that its larva is allied to the American philenor. It resembles a "partially ripe mulberry" as Pryer states and is by no means an orange-puppy. There are seven orange-family feeders in our fauna: P. xuthus, protenor, macilentus, maackii, bianor, helenus, and memnon. They are all members of the Fluted Papilios, among which the adult of macilentus alone somewhat resembles the alcinous ♂ (and the southern form of the ♀).

Tarō Iwase
Kanagawa-ken, Japan

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DECEASED

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