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Spectral Reflectance Characteristics of Butterflies (Lepidoptera) from Trinidad, B.W.I.[1]

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(Plates I-III; Text-figures 1-9)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, British West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe. (Zoologica, 1952, Vol. 37, No. 13, pp. 157-184.)]

CONTENTS

INTRODUCTION

ALTHOUGH butterflies are to human eyes among the most colorful members of the animal kingdom, little is yet known of the physical characteristics of the colors themselves. Similarly, the possible adaptive significance of colors and patterns in intraspecific insect behavior remains largely unexplored. Because of differences in human and insect vision, a study of the role of color in the social behavior of any species of butterfly must be built on a knowledge of the spectral composition of the various colors of its wings. Since butterflies, along with the majority of insects, are visually

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sensitive to the near ultraviolet, this short-wave region is also important. The present investigation of the spectral composition of certain butterfly colors, in both the visible and ultraviolet, was therefore undertaken as a prerequisite to the study of social behavior in these same species.

The colors of many butterflies depend not only on direct reflectance from pigment deposited in the scales, but also in part on the structure of the scales themselves. These physical colors, here classified as iridescent phenomena, may be caused by a variety of means—by the scattering, reflection and refraction of light from the scale surfaces, or by interference between reflections from superimposed, microscopic plates. Because of the prevalence of these non-pigmentary colors, absorption and transmission spectra of extracted pigments are not reliable bases for determining the portions of the spectrum which actually reach the insect eye.

The current problem, therefore, involved the working out of a practical method for recording the spectral composition of the colors, regardless of their origin. There were three important requirements to be met. The procedure must be able to give valid general analyses both of entire butterfly wings and of minute portions of patterns; it must be suitable for use by non-physicists working under tropical conditions with limited laboratory facilities; finally, it must also be applicable to fresh flowers and to fast-fading, non-lepidopterous insects, in connection with various other studies of behavior. The photographic method described in the following pages has met these requirements adequately.

In the present paper the term "reflectance" is used in its broadest sense, in opposition to "absorption" and "transmission," to include color phenomena caused not only by simple reflectance from pigment, but by any structural means as well.

Deep appreciation goes to Dr. Y. K. Roots of the Physics Department, New York University, who advised me on the general method, gave many most helpful suggestions and lent the use of his department's densitometer for negative analysis. Hearty thanks are also due to Mr. and Mrs. C. Reed Cary of Philadelphia for their gifts of interference filters, and to Messrs. John Duane and Daniel Smith, both of the Interchemical Corporation, New York, for providing ultraviolet spectrophotometric analyses of standards. Finally, I am particularly grateful to Dr. William Beebe, Mr. Henry Fleming and Miss Rosemary Kenedy of this Department for their help in the field and for advice in many particulars. All systematic identifications are through the kindness of Mr. Fleming.

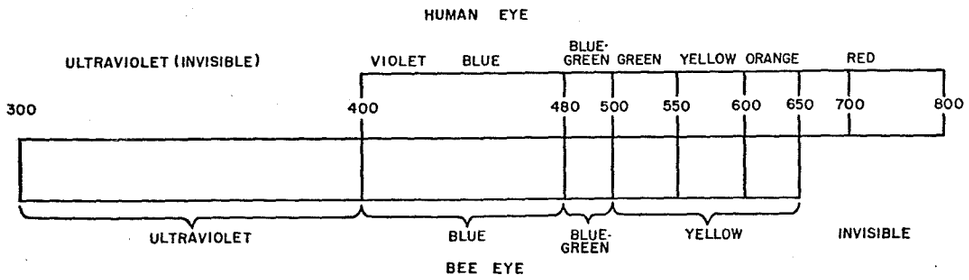
Historical Review

It appears that no one has yet published spectrophotometric reflectance curves from the natural wing surfaces of butterflies. The work most closely related has been concerned with butterfly patterns in general and with the pigments in the scales, from the points of view of their chemistry, physiological origin, development and, occasionally, of their possible application to problems of systematics. The following key references will give a survey of the subject: Cockayne (1924); Coste (1890-1891); Ford (1941-1947); Fox (1953); Hopkins (1895); Köhler (1926); Mayer (1896-1897); Mayer & Cook (1943); dos Passos (1948); Richards (1951); Schmidt (1942); Thomson (1926); Timon-David (1947); Wigglesworth (1924, 1946, 1949).

One of the first of these, Mayer (1897, p. 173), observed the colors of a few of the butterflies in his classic study by means of a small direct vision spectroscope, and noted, "In general it was found that the colors of the wings are not simple, but compound; that is to say, they are made up of a mixture of several different colors."

Some of the above references, notably Fox (1953) and Richards (1951), also discuss the physical characteristics of structural colors in butterflies and review the literature. Anderson & Richards (1942), Gentil (1942, 1943), Kühn (1946), Kühn & An (1946) and Suffert (1924) are entirely concerned with structural colors, either in butterflies alone or in insects including butterflies. The Anderson & Richards study of the interference colors of blue *Morpho* butterflies with the electron microscope is the most thorough ever made of such insect colors, and is invaluable for an understanding of the subject.

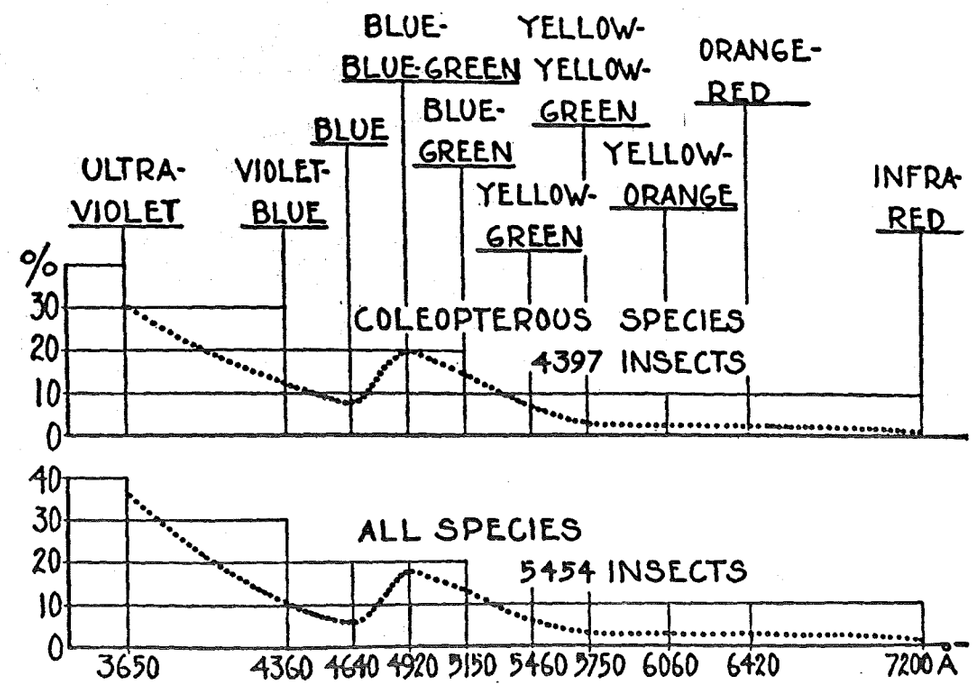
The photographic approach to analysis of butterflies' colors has apparently been used only twice—first by Lutz (1933.1) who published prints of a number of species taken through an ultraviolet filter. His purpose was to indicate how a butterfly's pattern might differ in appearance to another insect, sensitive to ultraviolet, in comparison with its appearance to human beings. However, he did not in his photographs take into account the fact that insects are also sensitive to practically all of the humanly visible spectrum, although at least most of them are only weakly sensitive to the orange and red. Brues (1941) accordingly photographed a series of butterflies not only through an ultraviolet filter alone but again for comparison, through a blue filter which both admitted some ultraviolet and cut off the orange and red. This arrangement, he considered, would thoretically give a rendition of the pattern which should approach in relative



TEXT-FIG. 1. Comparison of the visible spectrum for the human eye (above) and for the honeybee (below). (Redrawn after von Frisch, 1948, 1950). Wavelengths in millimicrons. Cf. Text-fig. 2.

values of light and dark that perceived by the insect. The high sensitivity of the negative material to ultraviolet rays, and the relatively low intensity of these rays in his particular source, would roughly compare, he suggested, with natural conditions: although the insect eye is extremely sensiitve to ultraviolet (Text-figs. 1, 2), little of this region penetrates the earth's atmosphere (Text-fig. 3). However, Brues' purpose was not to determine relative reflectance in the various spectral regions, or to any standard, and hence his discussion has no direct application to the present study.

As indicated above, the insects' sensitivity to the quality of light is inseparably connected with the problem of any adaptive evolution of their wing colors in intraspecific relations. Because of this connection, it seems desirable to give here a brief review of the current state of knowledge of this aspect of insect vision, so that the implications of the spectral analyses to be given may be more promptly clear. This is naturally divided into two sections: the first concerns the limits of the spectrum visible to insects, and the relative sensitivity of the insect to the various spectral regions. The second is concerned purely



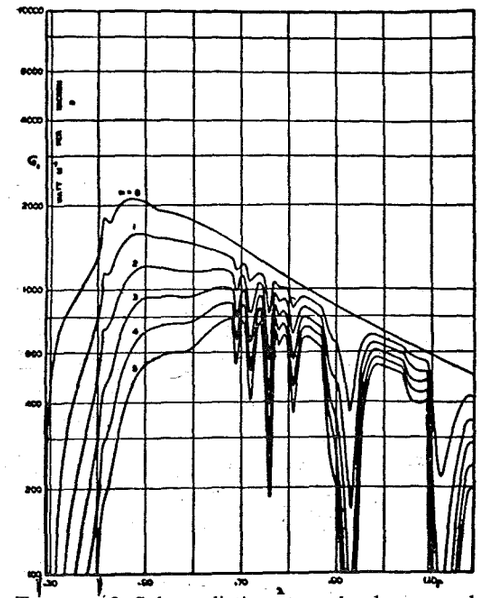
TEXT-FIG. 2. Group behavior curves of insects to colored lights. (From Weiss, 1943.) Wavelengths in Angstrom units. "All species" in the lower diagram included, in addition to the 4,397 Coleoptera shown in the upper figure, more than a thousand Diptera, Hemiptera and Hymenoptera.

with such perception or "color vision," including proof of differentiation of colors from all shades of gray, and the number of separate hues distinguished.

It has been known since the work of Sir John Lubbock (1882) that ants are not visually sensitive to the identical stretch of the electromagnetic spectrum which forms, for human beings, the visible spectrum. All insects which have since that time been adequately tested, including a number of Lepidoptera, have proved to be optically sensitive to the near-ultraviolet and many, at least, have very weak or negligible sensitivity in the orange-red and red. Weiss (1943.2, 1944, 1945, 1946) has published critical reviews of both early and recent work, with the emphasis on strictly laboratory experiments concerning the insects' responses to light of various colors. Ilse (1941) reviews work, including her own, on color vision in bees and butterflies based on observations and experiments either in the field or in insectaries, and involving the insects' behavior in seeking food, mates, etc.

For human beings in ordinary daytime vision there is a single peak of sensitivity in the yellow-green. For honey bees, *Drosophila,* many beetles and one hemipteron, tested by group behavioral responsiveness to light, it has been shown definitely that there are two peaks (Text-fig. 2). In all of these insects and probably in the vast majority, if not all, of other eyed insects, the major peak is in the near ultraviolet (Bertholf, 1931, 1932; Weiss, 1943.1; Weiss *et al.,* 1941, 1942), at least for more distant vision (Weiss *et al.,* 1941). In honey bees, according to other tests, the second, minor peak is in the yellow-green, similar to the single peak in man (Bertholf, 1931); this is not shown on Text-fig. 2. Without reference to the ultraviolet, Schlieper (1927) and Ilse (1932.1) gave evidence that between blue and red the peak of two species of nymphalid butterflies (*Vanessa*) is also in the yellow-green. In *Drosophila* and many beetles, however, the peak in the humanly visible region is in the blue-green or blue-blue-green (Bertholf, 1932; Weiss, *loc. cit.*; Weiss *et al., loc. cit.*). These peaks of sensitivity do not indicate in themselves that the insects have color discrimination; it is only that when large numbers are tested, by various means, the majority respond most readily to light of these particular wavelengths, when given a choice of other bands of equal intensity. Furthermore, when intensities are increased adequately, but not excessively, positive responses may be elicited all the way up to 720 mμ (Weiss, *loc. cit.*; Weiss *et al., loc. cit.*).

Electroretinograms of a grasshopper, a moth (*Samia cecropia*) and a beetle (*Dytiscus*) give



TEXT-FIG. 3. Solar radiation at sea level, proposed standard radiation curves (from Moon, 1940). Wavelengths in microns. Reproduced to show the sharp cut-off of ultraviolet (.30-.40μ) penetration to the earth with increase of air mass (m). The extent of the visible spectrum for insects is approximately .30μ to .65μ; for man, .40μ to .70μ. Cf. Text-figs. 1 and 2.

results comparable with the group behavior responses of beetles, *Drosophila* and Hemiptera cited above, the electroretinograms showing a major peak in the green (about 520 mμ); responses in the ultraviolet were not tested (Crescitelli & Jahn, 1939; Jahn & Crescitelli, 1939; Jahn & Wulff, 1948). A similar peak was shown in the electroretinograms of single visual cells of the horseshoe crab (*Limulus*) (Graham & Hartline, 1935). As Weiss sums up (1944, p. 271): "Thus it appears that both the electrical responses of the insect eye and the motor responses of the insect itself to different colors of equal intensity are due to differences in sensitivity, or to the absorption of light, which varies with wavelength, by the primary photosensitive substance of the visual sense cells, and are not the effect of wavelength by itself."

Only in honeybees has actual color discrimination in insects been thoroughly investigated. Thanks especially to the work of von Frisch (1915), Kühn (1927) and Lotmar (1933), it is well established that four separate hues are distinguished (Text-fig. 1): bee-ultraviolet (from about 300-400 mμ), bee-blue, covering the human violet and blue (400-480 or 490 mμ), bee-blue-green (480 or 490 to 500 or 510 mμ)

and bee-yellow, covering a long stretch of spectrum which, for human beings, is seen as green, yellow, orange and orange-red. (510-650 mμ). Furthermore, these four hues consist, for the bees, of two complementary pairs (Hertz, 1937.1, 1937.2, 1937.3, 1939). Just as red and blue-green, orange and blue, and yellow and violet are complementary for human beings, so is bee-ultraviolet complementary to bee-blue-green, and bee-blue to bee-yellow. Finally, because of their sensitivity to ultraviolet, "white" for a bee must include reflectance in the ultraviolet as well as throughout the visible. Many objects, including flower petals, male pierid butterfly wings and zinc oxide white pigment, all of which appear white to human beings, reflect virtually no ultraviolet and are distinct to bees, including meliponids (Lutz, 1933.2), from positively ultraviolet whites. They appear, in fact, to affect the bees in the same fashion as bee-blue-green, since the complementary components in the white, bee-blue and bee-yellow, "cancel out." A comparable situation exists for human beings where a surface strongly reflects light of all visible major hues save one—violet, for example; such a surface is seen as pale yellow; this, of course, is the complementary of the absent hue, lightened by the "cancelled out" complementaries of the remainder of the visible spectrum.

Work on color discrimination in butterflies is less complete than in honeybees, but some butterfly families have already been shown to have well developed color discrimination, which in some cases appears to be similar to that of bees. Ilse (1928), working with European butterflies, found that nymphalids distinguish at least three hues in the visible region—a "blue," "green" and a "yellow" which, as in bees, apparently does not extend much beyond the orange; the ultraviolet region was not included in this study. In addition, her experiments suggested strongly that in pierids and papilionids the spectrum is extended well into the red, though red is not necessarily for them a distinct hue; she also showed (1937) that for the cabbage butterfly (Pieridae) at least, violet, mauve or reddish is complementary to a blue-green-to-green hue, which would seem to exclude, for pierids, the possible complementariness of this green to ultraviolet.

Preliminary work of our own, not yet published, on butterflies in Trinidad proves that butterflies in general undoubtedly have high sensitivity in the ultraviolet, and that these butterflies include both pierids and papilionids, as well as nymphalids, morphids, heliconiids, ithomiids and danaids. Further, we corroborate Ilse's findings that butterflies decidely distinguish all hues, including non-ultraviolet white, from all shades of positively-ultraviolet gray. Work on spectrum extension into the red, the numbers of hues discriminated and their system of complementaries is still proceeding.

Using North American wildflowers as subjects, Lutz and Richtmyer inaugurated work similar to our own in their investigation of ultraviolet reflectance from flowers. Richtmyer (1923) used a small, portable quartz spectrograph, which was operated directly in the field. In a correlated study Lutz (1924) used ultraviolet, blue and red filters, combined with pinhole photography, for roughly determining spectral reflectance in the three regions. In both studies, suitable use was made of magnesium oxide standards for comparison. At that time the fact that bee-ultraviolet and bee-blue-green are complementary colors was not known, and hence the particular importance of the blue-green region. However, as it turned out, only four species out of 25 tested proved to reflect any possibly significant proportion of ultraviolet; these consisted of three yellow flowers and one rose-purple species. In 1933 Lotmar investigated European flower colors spectrographically in the laboratory, agreeing with Lutz's results in recording very low to negative ultraviolet reflectance in the vast majority of tested flowers. In Trinidad our own spectral examinations of tropical flowers have given similar results (unpubl.).

METHOD

All of the background summarized in the preceding section was borne in mind in working out the method used in this study. Some details are included which may seem over-obvious to physicists, and others which will appear equally uncalled for to a practicing zoologist. However, it is increasingly clear that when one profession tackles the techniques or materials of the other, the most elementary details are the ones which often cause the most time-consuming delays and preliminary mistakes.

The requirements of the method may be divided as follows:

1. It must be useful for color analyses of insects, flowers and leaves in general.

2. It would be necessary to determine spectral reflectance from the near ultraviolet to the red, covering the ultraviolet penetration of sunlight to the earth. Since both the penetration of sunlight and the transmission of bee ommatidia fall off sharply below 366 mμ, that figure was taken as an adequate lower limit for the required spectra. The shortest rays which reach the earth measure only 290 mμ; however, these are present in sunlight only under ideal weather conditions (Text-fig. 3). It was not necessary to secure measurements of exact reflectance at individual wavelengths, or at extremely narrow bands of

TABLE 1. FILTER COMBINATIONS USED IN SPECTRAL REFLECTANCE STUDY
(cf. Text-fig. 4)

Filters	Light Source	Color for Man	Approx. Transmission Range ($m\mu$) (under conditions used)	Peak ($m\mu$)	Remarks
Wratten 18 A	Sun	Black (UV)	290–400	366	
Wratten 18 A	"Mineral-light" SL 3660	Black (UV)	290–400	366	Peak of source extremely narrow
Wratten 18 A + Bausch & Lomb Interference KD 4002	Sun	Black (UV)	290–400	380	
Wratten 35(D) + 47(C5) + 2 A	GE Photoflood 2 A	Violet-blue	400–475	430	
Wratten 35(D) + 45(H)	GE Photoflood 2 A	Blue	430–475	450	
Wratten 75(n)	GE Photoflood 2 A	Blue blue-green	475–508	490	
Wratten 58(B2) + 45(H)	GE Photoflood 2 A	Blue-green	475–545	510	
Wratten 15(G) + 45(H)	GE Photoflood 2 A	Green	508–548	525	
Wratten 58(B2) + 15(G)	GE Photoflood 2 A	Green-yellow	506–615	540	
Wratten 58(B2) + 22(E2)	GE Photoflood 2 A	Yellow	548–618	570	
Wratten 25(A) + Bausch & Lomb Interference 600 $m\mu$	GE Photoflood 2 A	Orange	590–660	600	
Wratten 29(F)	GE Photoflood 2 A	Orange-red	600–650	640–660	Used in preliminary work only
Wratten 25(A) + Bausch & Lomb Interference 650 $m\mu$	GE Photoflood 2 A	Orange-red	590–660	650	

wavelengths; only the *relative* reflectance in *moderately* narrow spectral regions affects color discrimination. Man distinguishes up to 150 spectral hues. For bees, however, as has been said, there are only four; within the range of each of these four no discrimination appears to be made. For the same reasons, individual absorption lines, which are of vital importance in spectroscopy proper, may be disregarded; in behavior it is the general picture that matters.

3. The apparatus used in the field laboratory must be sturdy and not subject to special operational difficulties in a humid tropical climate.

4. Since the wings of many of the species to be studied had complex wing patterns and colors, and time for the problem was limited, the method chosen must be fairly rapid.

Three general approaches were possible:

1. *Spectroscopic.* A quartz instrument is essential for this method, because of the necessity of determining reflectance in the near ultraviolet, which is not sufficiently transmitted by ordinary glass. Suitable small instruments, such as described by Richtmyer (1923, p. 153) are apparently not being manufactured today. The search was early given up, however, because it was realized that, in the study of butterfly wings, many of the areas of greatest interest were too small to be readily analyzed by their reflected light, especially with the small instrument that would be taken to the field laboratory. Also, the simple photographic laboratory facilities available were not suitable for the delicate processing of spectographic plates.

2. *Spectrophotometric.* There were four disadvantages to this method, which, under ideal conditions, would be the best. First, even the largest and most modern instruments are not suitable for the analyses of the reflectance of very small areas; samples about 4 centimeters square are desirable, while those less than one centimeter square can scarcely be handled. The majority of our specimens, even flowers, do not meet these requirements. Second, it is difficult to control the scattering of light, especially in the short-wave end of the spectrum, in such samples of diffuse reflectance as insect wings. In these at least some of the color is often structural, instead of completely pigmentary. Also, because of the overlapping scales, the surface is not altogether smooth. Third, in humid tropical weather, spectrophotometers may need highly technical servicing which is not available; among non-physicist operators, the development of instrument untrustworthiness might not be promptly or easily detected, much less corrected. Fourth, except in the largest recording instruments, which are beyond the means of small research laboratories requiring only their occasional use, the analysis of each colored area may require many hours. Therefore, it was finally decided that the method was both too precise and yet too subject to error for field use by amateur spectrophotometrists for the rather coarse determinations desired. Zoological workers interested in the possible applications of spectrophotometry to their own problems will find in Harrison, Lord & Loofbourow (1948) a comprehensive introduction to the subject.

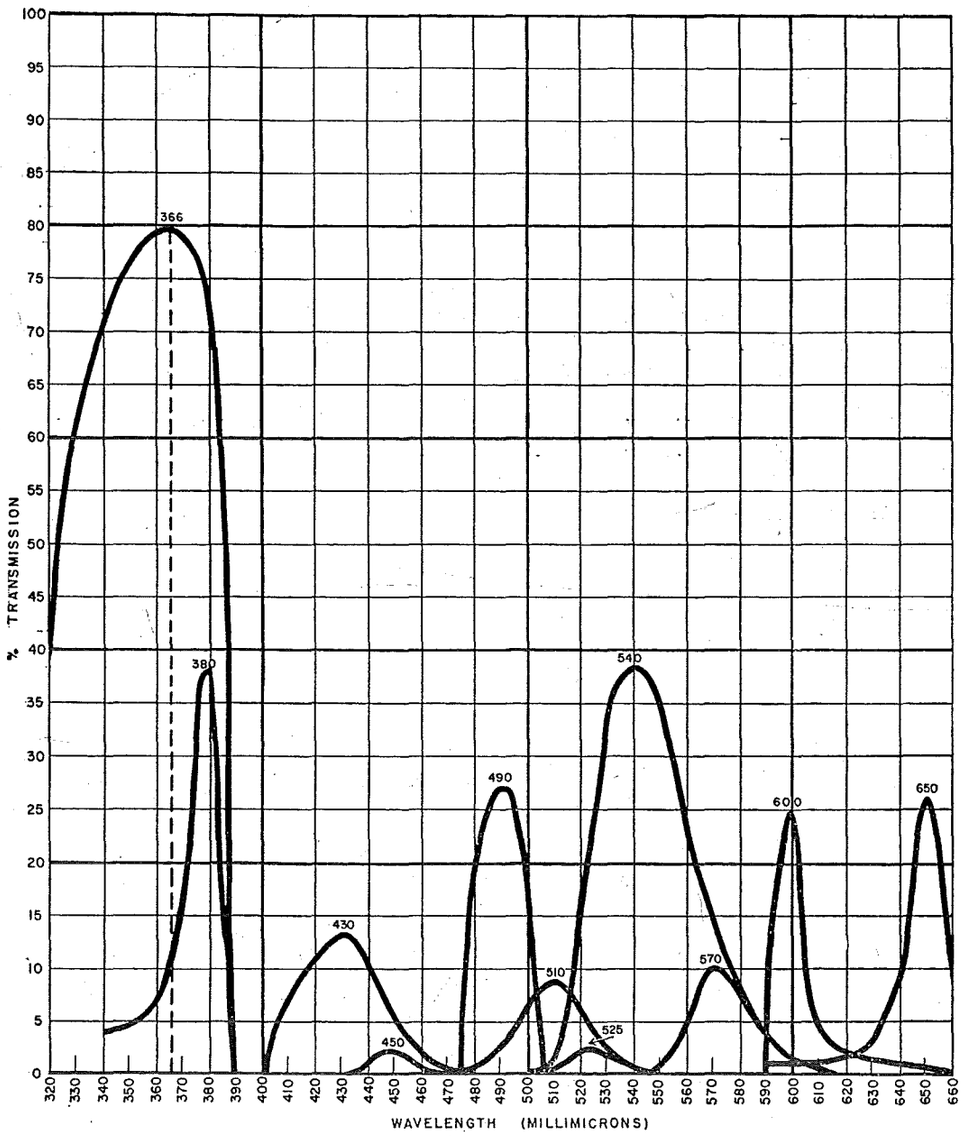
3. *Photographic.* For the reasons stated above, the relatively simple method of photographic filter analysis was selected. This is essentially an elaboration and refinement of that used by Lutz in his preliminary analysis of ultraviolet reflectance in flowers (1924).

The exact method eventually perfected in the present investigation is, in outline, as follows: Wings or parts of wings were photographed through a series of narrow-band-pass and interference filters and filter combinations (Table 1, Text-fig. 4). For preliminary surveys of several entire wings, crowded on single negatives at high reductions, a small area of magnesium oxide was included as a standard (Pl. II). This compound reflects a maximum of light falling on it of all wavelengths including the near ultraviolet. The densities of the photographed samples in each negative could then be roughly compared by visual inspection with the density of the magnesium oxide standard in the same frame. Small areas of color which appeared of special interest could subsequently be cut out of the wing, and rephotographed at higher magnifications.

For this second photographing, small samples were included in each negative of 19 Munsell neutral gray papers, ranging in value from "black" to "white." Upon our return to New York from Trinidad, the resultant negatives were analyzed by means of a microdensitometer, the reflectance of the specimens in each frame being matched in density with a gray sample of similar reflectance in the same frame (Pl. III). Spectrophotometric curves were secured for the gray scale (Text-fig. 5). Thus the reflectance of a given specimen at the points of peak transmission of the various filter combinations could then be read directly from these spectrophotometric curves. In this way a percentage was determined of the reflectance of the specimen in each spectral region. Obviously, the method is rough, when judged by the standards of modern spectroscopy. However, when applied with maximum care and with sufficient checks, the procedure has proved wholly adequate for our purposes. It has the advantage that prompt macroscopic inspection of the results may be made in the field, as a preliminary to experiments with hitherto untested species, without waiting for densitometric analysis. It is clear at once, for example, on any negative strip, whether or not any noteworthy amount of ultraviolet reflectance is present, and whether a certain red extends strongly down into the yellow-orange or yellow. If it does so extend, for those insects which are known to have weak sensitivity in the red region, the patch could still be strongly perceived as a hue. A second reason for analyzing the wings in the field rather than from mounted museum specimens is that the possible effects of drying and of chemical insecticides have been heretofore unkown.

The method will now be described in detail, along with the chief sources of error and the necessary precautions that must be observed.

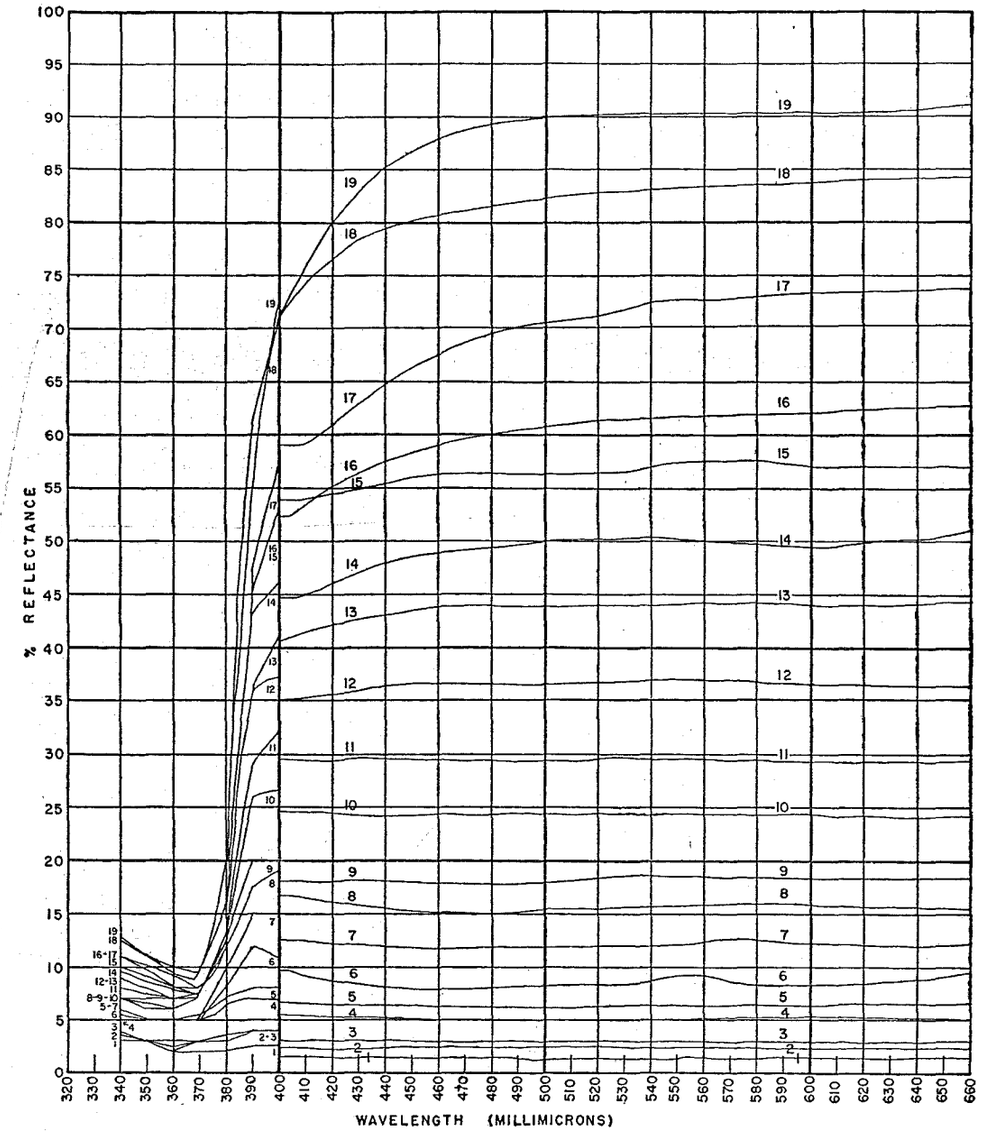
A. *Selection and Preparation of Material.* Except where the effects of aging and fading were being studied, fresh, unmarked specimens were used. Where possible, those less than four days out of the pupa were selected, which was often feasible, thanks to the Simla laboratory's insectaries (Crane & Fleming, 1953). The butterflies were killed by pinching the thorax, in order to eliminate possible effects of chemicals on spectral reflectance, and were photographed at once. When photography by sunlight was necessary, the desired areas of wing were cut out and, taking care to handle them only by the extreme edges with fine forceps, were attached to black matte paper with rubber cement; this was necessary because of the wind. Indoors, the specimens were simply arranged on black velvet, on a stage or table immediately beneath and at precisely right angles to the lens. All species discussed in this paper have been analyzed at least twice and frequently more often, at various magnifications, so that the results presented are well checked.



TEXT-FIG. 4. Transmission curves of filter combinations used in analyzing colors of butterfly wings. Redrawn from spectrophotometric curves furnished by the Electrical Testing Laboratories, and Bausch and Lomb Optical Co. See Table 1 for identification of filters. The vertical broken line at 366 mμ indicates position of the peak of output, a narrow band, of the ultraviolet lamp employed, "Mineralight" SL 3660, after a curve furnished by the manufacturer (Ultraviolet Products Co.).

B. *Magnesium Oxide Standard.* In the preliminary survey of entire wings under low power, a sample of white magnesium oxide was included along the edge of each negative. Since this compound reflects about 98 percent of visible light at any given wavelength, in both the visible and near ultraviolet, it is a convenient gauge of relative brightness of the objects photographed. When an attempt is made to photograph the standard in each negative of a series to a similar and fairly high density, the relative density of a given piece of wing photographed through each filter combination can be roughly estimated by inspection.

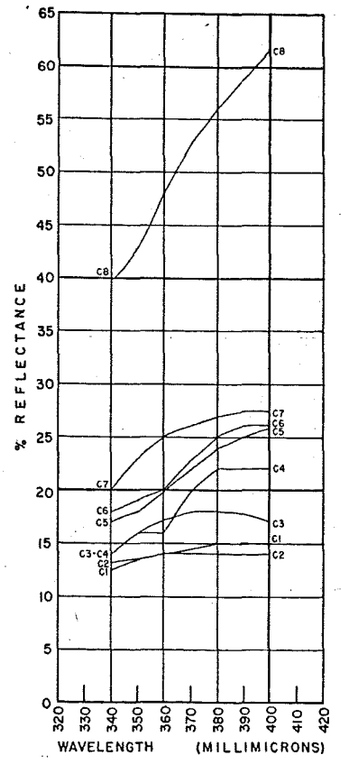
An example is given in Plate II, Fig. 42. The six frames, reading from left to right, were ex-



TEXT-FIG. 5. Reflectance characteristics of neutral gray papers used for comparison standards in butterfly color analyses. Redrawn from spectrophotometric curves furnished, in the visible, by the manufacturer, Munsell Color Co., and in the ultraviolet by the research laboratories of the Interchemical Corporation. The numbers from 1 to 19 indicate the individual papers from darkest to lightest, and correspond, in that order to the following Munsell identification numbers: N1, N1.5, N2, N2.5, N3, N3.5, N4, N4.5, N5, N5.5, N6, N6.5, N7, N7.5, N8, N8.5, N9, N9.2, N9.6.

posed through filters or filter combinations with peaks in, respectively, the ultraviolet, blue-violet, blue-green, green-yellow, yellow and orange-red. The left image in each negative frame represents the under wings of *Callicore aurelia,* in which most of the under forewing is red. Even in this printed reproduction, it is at once evident that the area has low reflectance in the ultraviolet and violet-blue, practically zero in the blue-green and yellow-green, low in the yellow and moderately high in the orange-red.

Accurate percentages, however, of reflectance in terms of magnesium oxide cannot be obtained by direct comparison of the densities of the spec-



TEXT-FIG. 6. Ultraviolet characteristics of certain Stoelting Psychological Test Papers for use in supplementing gray standards. Redrawn from spectrophotometric curves furnished by the research laboratories of the Interchemical Corporation. Correspondence of identification numbers: C1 = Stoelting No. 6; C2 = Stoelting No. 7; C3 = Stoelting No. 16; C4 = Stoelting No. 15; C5 = Stoelting No. 12; C6 = Stoelting No. 14; C7 = Stoelting No. 11; C8 = Stoelting No. 17.

imen with that of the standard through use of the densitometer. This is because of fundamental characteristics of the photochemical process, in which faint light affects the density of a negative relatively less than does strong light. As a result, length of exposure and time of development also have unequal effects on latent images of highly different potential densities; the necessary control of conditions, to insure uniformly of negative material and its processing and proper analysis of the results, was beyond the scope of the facilities at hand. Instead, a gray series, as described below, was included in each negative wherever exact numerical ratios were desired.

For use in the preliminary analyses, the magnesium oxide standard was prepared. The stainless steel blade of a table knife was coated with magnesium oxide in the following manner: A small heap of magnesium metal was ignited with matches. The knife was then easily coated in the smoke, which could be stimulated by poking the embers with a dissecting needle. The method, although simplicity itself, gave trouble to our group of non-chemists until we discovered that a heap of the metal, rather than a flat patch, is needed for easy ignition. The match should be thrust into a hollow at the top of the heap. The knife must be recoated at least every three days, if in daily use; if more seldom, immediately before every photographic session. The special standards which can be purchased from the U. S. Bureau of Standards for spectrophotometric work were not necessary for the rough results desired.

C. *Gray Standards.* In each negative intended for accurate analysis were placed samples of each of the 19 steps in the Munsell Neutral Gray series. They were attached to strips as follows: Small rectangles were cut from the gray papers, of such a size that in the finished negative each measured at least 2 mm across. Smaller sizes were difficult to measure on the densitometer, although samples as small as 1 mm square could be used where necessary. These rectangles were divided into two groups and attached with paper cement to two strips of cardboard; a number designating each step was written underneath in India ink, to be visible on the developed negative. Care was taken to handle the grays only by the edges and with forceps; the strips were kept in light-tight boxes in cellophane envelopes when not in use. In composing a frameful of sample wing areas under the lens, a strip was placed along one or both long edges of the field, the specimens being laid between them. This arrangement made for ease of comparison both by inspection and in the densitometer (Pl. III, Figs. 45-52).

Spectrophotometric analyses in the visible were obtained from the manufacturers of the actual gray papers used (the Munsell Color Co., Baltimore, Maryland). The ultraviolet reflectance of the papers was furnished, from 340 to 400 mμ, by the Research Laboratories of the Interchemical Corporation (Text-fig. 5). Since reflectance in this region proved to be exceedingly low, with sharp drops below the violet, they were supplemented for ultraviolet exposures by a series of seven colored rectangles, selected for their progressively higher ultraviolet reflectance curves, from the Stoelting Psychological Color Test series (Pl. III, Figs. 45, 46). Their ultraviolet reflectance curves were also obtained from the Interchemical Corporation (Text-fig. 6).

D. *Camera and Lenses.* The most satisfactory set-up proved to be a Leica camera equipped

with a reflex housing and the front element of the 135 mm Elmar lens fastened to the Leitz bellows attachment. This assembly, in conjunction with a "Highboy" tripod, gave maximum ease of focussing and adjustment, under the circumstances, since the set-up could not be left indefinitely in place because of other uses for the equipment. A maximum magnification of 1:1.1 was obtained without the addition of extension tubes. The minimum area which could be accurately analyzed in the standardly equipped densitometer was about 1 mm square. The density of the smaller lines and spots could be roughly gauged by inspection. The specimens and comparison material were placed on a piece of black velvet beneath and at right angles to the vertically-aligned camera. A 90 mm Elmar lens in combination with extension tubes and a ground-glass focussing assembly were also used with success, although this set-up proved much less convenient. Both the 90 mm Elmar and the 135 mm Elmar adequately transmitted ultraviolet in the desired region.

E. *Filters.* During the first season of 1950, a preliminary series of six combinations of Eastman Wratten filters was used. With appropriate substitutions and additions, this was expanded between 1951 and 1953 into a series of twelve combinations, including three Bausch and Lomb interference filters. The latter, used in conjunction with Eastman filters, transmitted with a narrow peak at 380, 600 and 650 mμ, respectively. They proved to be a satisfactory answer to the problem of isolating narrow bands in these regions, which could not be adequately dealt with by combinations of the regular glass and gelatin filters. The transmission curves of the combinations of the actual filters used were secured from the Electrical Testing Laboratories (Table 1, Text-fig. 4). The filters were attached to the camera by double or triple adapters when in use; at other times they were kept tightly closed in boxes. The basic tests were made within five months of the time the filters were spectrophotometrically analyzed. The selected filters are designated by the manufacturer as moderately stable and very stable. Their curves compare extremely closely with those furnished by Eastman in "Wratten Light Filters" (Anon., 1945).

F. *Film.* Throughout the series, Eastman 35 mm Plus X film was used. In this film, the spectral sensitivity extends far into the ultraviolet but, at the exposures used, not beyond 650 mμ in the red. Since no frame was being compared directly with any other frame, but only with a gray sample of similar density within the same frame, no special precautions were necessary to insure uniformity of the film used, temperature at which it was stored, etc.

G. *Illumination.* (Pl. III, Fig. 53). For the visible part of the spectrum, a single General Electric 2A photoflood lamp, with built-in reflector, was used. Because of the small size of the field, one lamp proved sufficient for even illumination. It was placed at an angle of 45 degrees to the camera-specimen axis, at a distance of 2½ to 3 feet from the specimen. Extreme care was taken to maintain this angle, in order to avoid direct reflectance of the light from any smooth scale surfaces into the camera, which of course occurs when a lamp is placed close to the camera-subject axis—that is, close to a 0° angle of incidence. In the early tests, before adequate precautions were taken, high reflectances were sometimes recorded in regions which, when properly tested subsequently, showed almost negative results.

The 45° angle of incidence was also maintained for areas in which the color was due at least partly to the structure of the scales. In the red of *Callicore, Biblis* and *Papilio,* for example, the iridescent effect was scarcely visible at this angle. (see p. 108). In strongly iridescent areas (*Morpho, Caligo*), the selected angle resulted in a preponderance of moderately short waves of moderate intensity; if the angle had been decreased, the result would have been a higher intensity of color with a preponderance of somewhat longer wavelengths, in accordance with the laws governing interference colors (e.g., Richards, 1951, p. 197 ff.; Fox, 1953, p. 56 ff.; and present paper, p. 109).

Lamps were replaced frequently, that is, before their weakening necessitated changed exposures. A black cloth hung between camera and lamp in the otherwise darkened room, and an effective sunshade, minimized the problem of scattered light. Incidentally, the cloth, even though black, protected the camera from the heat of the nearby lamp.

For the ultraviolet region, exposures under both a lamp and sunlight were made. The lamp was a model SL3660 "Mineralight" manufactured by Ultra-Violet Products Inc., South Pasadena, California. It had a narrow peak output at 366 mμ. Its use in conjunction with the Wratten 18A filter assured a limitation of the light to the desired region. The lamp was mounted on a horizontal standard which could be swung into position, replacing the Photoflood, for the 366 mμ ultraviolet exposure in each series; the same precautions to ensure a 45° angle are of course as essential as in the case of the visible light.

All specimens were also checked in bright sunlight, in combination first with the 18A filter,

giving a rather broad ultraviolet transmittance band, and second with this filter combined with an interference filter transmitting at 380 mμ. This combination of indoor and outdoor work insured against failure to discover strong areas of ultraviolet reflectance between 366 mμ and the visible. The outdoor work was restricted to those checks and to some preliminary surveys, because of the great difficulties due to breezes, changing light and stray reflections. In the final ultraviolet checks outdoors, the photography was confined to bright sunshine in mid-morning or mid-afternoon, in the middle of a wide-open gray-slate terrace. Even under these optimum conditions, however, scattered ultraviolet light was such a large factor out-of-doors, that strongly iridescent areas could yield no reliable comparative data and so are omitted from Table 3. These sunlight records of iridescent and partly iridescent surfaces were, however, useful in giving some ultraviolet maxima recorded under natural lighting conditions, and are included in the systematic section under the species concerned. Even areas of partly structural white, such as the wings of *Eurema albula,* were impossible to light evenly out-of-doors, as is shown in Pl. III, Fig. 45.

H. *Exposures.* The exposures by artificial light with the various filter combinations varied from 1/20 sec. to 30 sec. at stops of f 5.6 to f 8. The aim was simply to obtain an image of the desired specimen, at each filter combination, dense enough for easy comparison in the densitometer with the standard gray samples appearing in the same negative. This method obviated the necessity for attempting to equalize densities in respect to a magnesium oxide standard. As has already been mentioned (p. 93), a simple comparison of the density of an image of the specimen to that of a magnesium oxide standard in each negative could not be made to yield accurate results. Hence the necessity of using the gray series. Satisfactory sunlight exposures were around ⅛ sec. at f 9 for the 18A filter, ¼ sec. at f 9 for the 380 mμ interference filter in conjunction with the 18A filter, all being made with the bellows almost fully extended.

I. *Development.* All negative strips were developed in a roll-type tank in Eastman Microdol at standard times and temperatures with the usual precautions to obtain fine grain and even development.

J. *Densitometer.* The Welsh Densichron was used for eventual analysis of the negatives, the minimum aperture being selected for passing the beam of light up through the stage. This permitted, as described earlier, density readings from areas measuring a minimum of 1 mm square. It was found helpful to slip a piece of white paper temporarily between the negative and the aperture, for ease in the precise centering of tiny crucial areas above the slender beam of light. Several readings were taken for each area and, in the event of slight differences, the range recorded; the results were matched as closely as possible with a sample gray in the same negative, its reading being also noted as either more or less than that of the specimen. Because of the uneven nature of butterfly wings and their scales, it was sometimes necessary to use cautious judgment in selecting as typical a particular tiny area of a fairly large negative image for densitometric analysis; this was especially true of whole wings, which could seldom be completely flattened, and was an especial problem, because of the increased difficulty with scattered light, in ultraviolet photography out-of-doors (see under *Illumination* and Plate III, Fig. 45).

The final step was the determination of the percentage reflectance of the sample in each spectral region in terms of magnesium oxide. This was accomplished merely by reading, from the spectrophotometric curves of the Munsell gray samples, the percentage reflectance in each matching sample at the point of peak transmission by the filter combination used for a particular negative. In the case of high ultraviolet reflectance, the spectrophotometric curves of the selected Stoelting colors (p. 94) were consulted instead of the Munsell gray series.

Systematic Section

Note: The terms "negative reflectance," "negatively ultraviolet," etc., are used to denote reflectance values lower than the reflectance in the corresponding spectral region of the darkest standard gray paper—that is, less than 1.5% of the reflectance of magnesium oxide (see Text-fig. 5).

Black areas show negative reflectance in the ultraviolet, just as in the visible; they will not be mentioned in this section.

"Positively ultraviolet white" indicates high reflectance in the near ultraviolet, approaching that of magnesium oxide in this region, and approximately equal to the specimen's reflectance in the visible.

FAMILY DANAIDAE

Danaus plexippus megalippe (Huebner)
(Plate I, Figure 1)

Lycorea ceres ceres (Cramer)
(Plate I, Figure 2)

The spectral characteristics of these two species are practically identical and may be listed as follows:

1. The small white spots on the margins of the wings and on the thorax are very strongly positively ultraviolet, with comparable reflectance throughout the spectrum. Therefore, these whites are "pure" for these ultraviolet-sensitive insects.

2. In both the browns and the yellows, the ultraviolet reflectance is negligible on the upper wing surfaces, ranging from negative to less than 4%, the higher values occurring in ♀♀. In both sexes the reflectance is higher on the underwings than on the upper, corresponding to their paler coloration in the visible region.

3. Violets and blues are negative in both the browns and yellows.

4. The yellows take their first strong upward curve in the low blue-green, about 490 mμ; the browns on the other hand do not reflect markedly until around 525 in the green.

5. In the longer wavelengths, from 590 to 650, both yellows and browns reflect strongly, although the yellow is stronger than the brown except up in the orange-red where they finally approach equality.

6. For practical purposes, therefore, these yellows differ from the browns, first, in including a moderately strong blue-green component and, second, in their generally higher reflectance in the green, yellow and orange. The colored abdominal streaks do not differ noticeably in spectral composition from those of the wings.

FAMILY ITHOMIIDAE

Tithorea mopsa megara (Godart)
(Plate I, Figure 3; Plate II, Figure 43, right image in each frame)

Mechanitis doryssus veritabilis Butler
(Plate I, Figure 4)

Hypothyris euclea euclea (Godart)
(Plate I, Figure 5)

Hypoleria ocalea
(Doubleday, Hewitson & Westwood)
(Plate I, Figure 6)

Ithomia drymo pellucida Weymer
(Plate I, Figure 7)

Hymenitis andromica trifenestra (Fox)
(Plate I, Figure 8)

These six species are divided by color into two groups. The first four include all those combining brown, yellowish and black in their patterns, and usually having small white marginal spots. In spectral characteristics they are practically identical with the danaids described above.

The second group, composed of the largely transparent *Ithomia* and *Hymenitis,* show no interesting color characteristics. The transparent areas do not reflect ultraviolet (except, of course, when the membrane directly reflects incident light); the terminal white forewing spots and body spots of *Hymenitis* and the single forewing spot of *Ithomia* are positively ultraviolet. The brown marginal markings of both species are negatively ultraviolet.

FAMILY SATYRIDAE

Euptychia hermes (Fabricius)
(Plate I, Figure 9)

Euptychia hesione (Sulzer)
(Plate I, Figure 10)

The above two species of the genus *Euptychia* are typical in general appearance of the numerous local species of inconspicuous brownish wood nymphs. These, in addition to four other species examined more cursorily, show similar spectral reflectance characteristics. Because of their lack of spectral interest and variety the group was not analyzed in detail. All of their whites and very pale colors are positively ultraviolet, including the perimeters and highlights of the ocelli. The browns are typical of that color, showing practically negative reflectance in the ultraviolet, violet, blue and blue-green, and moderately weak reflectance in the longer wavelengths.

FAMILY HELICONIIDAE

Heliconius numata ethilla Godart
(Plate I, Figure 11; Plate II, Figure 43, left image in each frame)

Browns, yellows and white spots indistinguishable from those of the danaids (p. 96) and similarly colored ithomiids (above) previously discussed.

Heliconius melpomene euryades Riffarth
(Table 3)

Heliconius erato hydara Hewitson
(Plate I, Figure 12; Plate III, Figure 46; Text-figure 9a; Tables 2, 3)

The characteristics of the red forewing band of the very common *H. erato hydara* and of the locally exceedingly rare *H. melpomene euryades* appear identical, both to the human eye and in spectral reflectance, as does the corresponding pale pinkish band of the underside. Therefore the two species are here considered together. The reddest and brightest bands were Scarlet Red (Ridgway).

Reflectance in the ultraviolet is uniformly low, regardless of sex, freshness or narrow spectral band. The gross variation is from negative reflectance to 5%. The average reflectance from 10 specimens of *H. erato* (6 ♂♂, 4 ♀♀) is about 2.5% or less. The higher reflectances are sometimes found in the 366 mμ band, sometimes in

the 380 mμ band; 5% was attained twice: once by a moderately worn ♀, analyzed only after two years, at the 380 mμ band, and once by a ♂, freshly emerged and promptly photographed, at the 366 mμ band. The minima were found in similar extremes of the material—worn but promptly photographed ♀♀, fresh ♂♂ photographed after two years, etc.

The reflectance continues very low (less than 2%) through the violet, blue, blue-green and green, the blue-green (490-510 mμ) invariably registering minimum readings.

In the yellow-green (around 540 mμ) the reflectance mounts to about 3%, and from there on there is a steady rise to about 30% in the orange-red (650 mμ).

No sexual differences have emerged. The noticeably oranger red (often Peach Red of Ridgway) of older specimens is recorded in the spectral analyses by slightly higher readings in the yellow and orange. However, the rise does not begin at shorter wavelengths, or, in other words, faded specimens do not reflect blue-green any more than do fresh ones.

The underwing band, more or less pinkish white to the human eye, often unevenly so, strongly reflects all wavelengths including the ultraviolet, with a very slight rise at the long end of the spectrum. (*Note*: The underwing bands in Surinam specimens of *H. erato* and *H. melpomene* are much redder than in the Trinidad forms and have low reflectance in the ultraviolet).

The red dots near the bases of the underwings are indistinguishable from the upper forewing band. The yellow streaks on the head, thorax and along the basal fore margin of the under hindwing are negatively ultraviolet, and resemble in general reflectance pattern the upper forewing band of *H. sara* (see below).

Heliconius sara rhea Cramer

(Plate I, Figure 13; Plate III, Figures 47-50, 2nd image from left in each frame; Text-figure 8a; Tables 2, 3)

Yellow spots on upper forewing: (Usually Martius Yellow of Ridgway). Ultraviolet almost negative, violet low, blue moderate, a sharp climb in the low blue-green which then holds almost level at around 50% through the orange-red, there being a slight maximum in the yellow-green and yellow.

Iridescent blue on hindwing: (Blue Violet to Hyacinth Blue of Ridgway). Moderate and about equal reflectance in the ultraviolet, violet and blue; reflectance reduced but present in blue-green, practically negative at longer wavelengths.

Yellowish white on lower forewing and on body: Strong reflectance at all wavelengths, including ultraviolet.

Red dots on lower hindwing about as in *H. erato hydara*.

No conspicuous sexual differences.

Heliconius ricini insulana Stichel

(Plate I, Figure 14; Plate III, Figures 47-50, 3rd image from left in each frame; Text-figure 9b; Tables 2, 3)

Yellow spot of upper forewing: (Martius Yellow of Ridgway). Similar to that of *H. sara rhea* (see above).

Red area of upper hindwing: (Scarlet Red of Ridgway). Similar to the forewing red band of *H. erato hydara* (p. 97).

Pale yellowish markings of underwings and body: As in *H. sara rhea*.

Heliconius aliphera aliphera (Godart)

(Plate I, Figure 15; Plate II, Figure 44, left image in each frame)

Orange of upper wings: (Zinc Orange of Ridgway; dull specimens Tawny). Reflectance practically negative in the shorter wavelengths, including the ultraviolet, through the blue-green; a steep rise starts in the green and continues through the yellow, orange and orange-red.

Paler undersides of wings similar except for the usual moderate reflectance throughout the shorter wavelengths including the ultraviolet.

Dryas julia julia (Fabricius)

(Plate I, Figure 16; Text-figure 8b; Tables 2, 3)

Orange of upper wings: (Orange Rufous to Ochraceous Orange of Ridgway). Practically identical with *H. a. aliphera* (see above), except that the richest areas in fresh specimens tend to have higher values in the orange and red.

Undersides of wings about as in *H. a. aliphera*.

Agraulis vanillae vanillae (Linnaeus)

(Plate I, Figure 17; Plate II, Figure 44, middle image)

Orange of upper wings: (Orange Rufous to Zinc Orange of Ridgway). Practically identical with *H. a. aliphera* and *D. j. julia* (see above) except that there is somewhat higher reflectance in the yellow-green and yellow.

Undersides of wings: The silvery-white spots reflect maximally in all regions including the ultraviolet. Remainder of surface about as in *H. aliphera*, except that there is almost negative reflectance in the ultraviolet and violet.

FAMILY NYMPHALIDAE

Phyciodes ofella ofella (Hewitson)

(Plate I, Figure 18)

Phyciodes leucodesma (Felder)

(Plate I, Figure 19)

The whites in both species are positively ultraviolet; the brownish blacks are unremarkable.

Victorina steneles steneles (Linnaeus)

(Plate I, Figure 21; Text-figure 7c; Table 2)

Green of upper wings: (Light Yellow Green to Lumière Green of Ridgway, fading to Oural Green and Lichen Green). Reflectance in all specimens moderately low (8%) in ultraviolet, very low in violet and blue, and more than equal to ultraviolet in the blue-green. Nearly equal maxima extend from the green through the orange, with a slight decline in the orange-red. Faded specimens show slightly higher values in the visible short-wave regions.

Pale green of under wings similar to that of upper, but with higher reflectances throughout.

Ochraceous Orange (Ridgway) markings of under wings with negative reflectance at wavelengths shorter than green.

White markings positively ultraviolet.

Biblis hyperia (Cramer)

(Plate I, Figure 22; Text-figure 9c; Table 2)

Red of upper hind wing: (Scarlet Red of Ridgway, fading to Scarlet; a faintly iridescent blue film). Reflectance in ultraviolet higher than in any other region except yellow through orange-red; violet and blue moderately low; blue-green negative; green low; yellow-green moderately low; a sharp climb starting only at orange, continuing through orange-red. At larger angles of incidence there is a much higher—up to 20%—reflectance in the ultraviolet, which is indicated in the visible only by the transparent bluish structural sheen overlying the red pigment. The iridescent sheen is more apparent in some individuals than in others.

Colobura dirce dirce (Linnaeus)

(Plate I, Figure 24)

Dynamine theseus (Felder)

(Plate I, Figure 25)

Dynamine artemisia (Fabricius)

(Plate I, Figure 26)

The whites are positively ultraviolet and the browns unremarkable in all three species.

Adelpha cytherea insularis Seitz

(Plate I, Figure 28; Plate II, Figure 42, image at right in each frame)

Adelpha iphicla daceleia Fruhstorfer

(Plate I, Figure 27; Plate II, Figure 52, middle image in each frame)

In both species the slightly opalescent whites of the upper wing surfaces are positively ultraviolet. Orange (Mars Yellow of Ridgway) markings negative in ultraviolet and violet; a rise in reflectance starts in the upper blue-green; reflectance strong from yellow-green through orange-red.

Browns and undersides unremarkable.

Protogonius hippona trinitatis Rober

(Plate I, Figure 29)

Browns spectrally closely similar to those of the danaids, ithomiids and heliconiids.

Callicore aurelia (Guenée)

(Plate I, Figure 23; Plate II, Figure 42, left image in each frame; Text-figure 9d; Table 2)

Predominantly greenish iridescence of upper forewing: (Visually ranging from pale blue to green yellow). A typical spectral pattern, with angle of incidence at 45°, shows moderate reflectance in the ultraviolet and violet, while the level is twice as high and about equal from the blue throughout the orange-red, except for a dip in the blue-green.

Red of under forewing: (Spectrum Red to Rose Red of Ridgway, with overlying bluish structural film). Ultraviolet reflectance low to moderately low, the higher values at larger angles of incidence, violet low, blue moderately low, blue-green and green negative, green-yellow and yellow low; a very sharp climb starts in the orange and continues upward through the orange-red.

White of under hindwing: Positively ultraviolet.

Anartia amalthea amalthea (Linnaeus)

(Plate I, Figure 20; Text-figure 7d; Tables 2, 3)

Orange-red of upper wings: (Brazil Red of Ridgway, fading through Orange Rufous to Apricot Buff). Spectral reflectance negative in ultraviolet, regardless of whether fresh or faded; violet and blue very low; blue-green and green negative, green-yellow and yellow very low; a steep rise starts abruptly in the orange, and levels off in the orange-red. Faded specimens show higher values in the greens and yellows.

Browns of undersurfaces unremarkable.

FAMILY MORPHIDAE

Morpho peleides insularis Fruhstorfer

(Plate I, Figure 30; Text-figure 7a; Table 2)

TABLE 2. REPRESENTATIVE SPECTRAL REFLECTANCE PATTERNS OF SELECTED BUTTERFLY WING AREAS
(See also Text-figs. 7-9 incl.)

Subject [1]	Location	Color	% Reflectance (mμ) [2]									
Peak transmission of filter combinations (see Table 1 & Text-fig. 4)			366 [3]	430	450	490	510	525	540	570	600	650
HELICONIIDAE												
Heliconius erato ♂	upper forewing	red	3.5	2	2	neg.	neg.	2	3	9	19	29
Heliconius erato ♀ (faded)	upper forewing	red	1.5	2	2	neg.	neg.	4.5	5	14	19	29
Heliconius sara ♂	upper forewing	yellow	3	9	25	37	48	49	52	50	48	48
Heliconius sara ♀	upper forewing	yellow	3	8	20	44	48	48	50.5	47	45	44
Heliconius ricini ♂ (faded)	upper forewing	yellow	3	11	19	17	44	40	30	35	38	31
Heliconius ricini ♂	upper hindwing	red	2	neg.	2	neg.	neg.	1.5	6.5	12	22	31
Dryas julia ♂	upper forewing	orange	neg.	neg.	neg.	neg.	neg.	7	19	24	27	38
NYMPHALIDAE												
Victorina steneles ♂	upper forewing	green	8	3	4	9	15	18	20	20	20	18
Biblis hyperia ♂	upper hindwing	red [4]	9	3	5	neg.	neg.	2	6.5	9	29.5	36
Callicore aurelia ♀	under forewing	red [4]	6	3	5	neg.	neg.	neg.	2	3	14	40
Callicore aurelia ♀	upper forewing	green [5]	12	13	25	17	25	26	26	26	25	23
Anartia amalthea ♂	upper hindwing	red	neg.	3	2	neg.	neg.	neg.	5	3	21	25
MORPHIDAE												
Morpho peleides ♂	upper forewing	blue [5]	16	30	38	21	20	20	12	8	8	2
BRASSOLIDAE												
Caligo illioneus ♂	upper hindwing	violet [5]	11	5	13	6	5	5	5	4.5	3.5	2.5
PAPILIONIDAE												
Papilio neophilus ♂ (faded)	upper forewing	green	neg.	9	15	12	17	16	17	14	19	14
Papilio neophilus ♂	upper hindwing	red [4]	9.5	2	neg.	2	1.5	neg.	3.5	9	24	33
Papilio neophilus ♀	upper hindwing	red [4]	14	10	8.5	neg.	neg.	neg.	1.5	5	18	24
Papilio anchises ♂ (30 yrs. old)	upper hindwing	red [4]	3	7	4	neg.	neg.	2	4	6	24.5	40
Papilio anchises ♀	upper hindwing	red [4]	5	4	3	neg.	neg.	2	3.5	10	25	47
Papilio anchises ♀ (1 yr. old)	upper hindwing	red [4]	3	3	5	neg.	neg.	2	3	9	20	35
Papilio anchisiades ♂	upper hindwing	red [4]	9	7	5	2	2	2	4	8	18	24.5
Papilio anchisiades ♀	upper hindwing	red [4]	8	5	5	2.5	2	4	5	9	15	24.3
Papilio thoas ♂	upper hindwing	yellow	neg.	2	6	11.5	15	19	21	27	29	29
PIERIDAE												
Anteos maerula ♂	upper hindwing	yellow	neg.	neg.	2	24	38	42	42	44	46	49
Anteos maerula ♂	under hindwing	yellow	5	10.5	12	18	25	27	28	28	26	18
Phoebis sennae ♂	upper hindwing	yellow	2	3	9	36.5	36.5	49	50.5	50.5	61.5	44
Phoebis sennae ♂	under hindwing	yellow	6	11	14	36.5	36.5	50	52	52	56	42
Phoebis sennae ♀	upper hindwing	yellowish	17.5	25	27	25	25	29	29.5	33	30	28
Phoebis sennae ♀	under hindwing	yellowish	7	22	22	24	21	26	29	28	29	26
Melete lycimnia ♂	under forewing	white	5	38	44	52	55	53	50	58	62	70
Melete lycimnia ♂	under hindwing	yellow	neg.	8	15	46	47	47	48	57	60	68

[1] For subspecific names see Contents, p. 85, or systematic section. All specimens freshly killed and unfaded unless otherwise stated.

[2] "Neg." indicates less than 1.5%.

[3] Source = "Mineralight" SL 3660 lamp. See text, p. 95; cf. Table 3.

[4] Color due to red pigment overlaid with iridescent film. Spectral pattern given is typical for specimens lighted at usual angle, emphasizing pigment rather than iridescence; see text p. 95.

[5] Highly iridescent. Spectral pattern given is typical for specimens lighted at usual angle; see text p. 108.

TABLE 3. REFLECTANCES IN THE ULTRAVIOLET OF SELECTED BUTTERFLY WING AREAS
Photographed by Sunlight Only

	Locality	Age or condition	Time since killed	Exposed to Paradichlorobenzene	Area	Color	% reflectance with Wratten filter 18A (peak: 366 mμ)[1]	% reflectance with Wratten filter 18A + Bausch & Lomb interference filter (peak: 380 mμ)
HELICONIIDAE								
Heliconius melpomene ♂	Trinidad	unfaded	1 month	No	upper forewing	Red	Neg.	Neg.
Heliconius erato ♂	Trinidad	2 days emerged	just killed	No	upper forewing	Red	3.5	3
Heliconius erato ♂	Trinidad	unfaded	2 years	Yes	upper forewing	Red	3.5	3
Heliconius erato ♂	Trinidad	faded	1¼ year	Yes	upper forewing	Red	3.5	3
Heliconius erato ♂	Surinam	unfaded	1 month	Yes	upper forewing	Red	Neg.	Neg.
Heliconius erato ♀	Trinidad	2 days emerged	just killed	No	upper forewing	Red	2	2
Heliconius erato ♀	Trinidad	unfaded	2 years	Yes	upper forewing	Red	4	4
Heliconius erato ♀	Trinidad	faded	2 years	Yes	upper forewing	Red	1.5	2
Heliconius sara ♀	Trinidad	unfaded	just killed	No	upper forewing	Yellow	Neg.	Neg.
Heliconius sara ♀	Trinidad	unfaded	2 years	Yes	upper forewing	Yellow	Neg.	Neg.
Heliconius sara ♂	Trinidad	unfaded	just killed	No	upper forewing	Yellow	5	5
Heliconius ricini ♂	Trinidad	unfaded	2 years	Yes	upper hindwing	Red	Neg.	Neg.
Heliconius ricini ♂	Trinidad	unfaded	just killed	No	upper hindwing	Red	Neg.	Neg.
Dryas julia ♂	Trinidad	2 days emerged	just killed	No	upper forewing	Orange	Neg.	Neg.
NYMPHALIDAE								
Anartia amalthea ♂	Trinidad	unfaded	just killed	No	upper hindwing	Red	Neg.	Neg.
PAPILIONIDAE								
Papilio thoas ♂	Trinidad	unfaded	2 years	Yes	upper hindwing	Yellow	Neg.	Neg.
PIERIDAE								
Eurema albula ♂	Trinidad	unfaded	just killed	No	upper forewing	White	Neg.	Neg.
Eurema albula ♂	Trinidad	unfaded	just killed	No	under forewing	White	5	8
Eurema albula ♀	Trinidad	unfaded	just killed	No	upper forewing	White	9	9
Eurema albula ♀	Trinidad	unfaded	just killed	No	under forewing	White	15	16

[1] "Neg." indicates less than 1.5%.

Iridescent blue of upper wings: A typical spectral reflectance pattern, photographed with the usual angle of incidence of 45°, shows the highest values in the violet and blue; values are from about three-fifths to two-thirds as high in the ultraviolet and from the blue-green through the green; reflectance moderately low from the green-yellow through the orange, dropping almost to negative in the orange-red. Greater or lesser angles of incidence increase the intensities in the regions of shorter or longer wavelengths, respectively.

Undersurface, including ocelli, unremarkable, the whites being positively ultraviolet.

FAMILY BRASSOLIDAE

Caligo illionéus saltus Kaye

(Plate I, Figure 31; Text-figure 7b; Table 2)

Iridescence of upper wings: (Visual range from dull violet to dull blue). A typical spectral reflectance pattern, photographed as usual with an angle of incidence of 45°, is highest in blue, next highest in ultraviolet. Values one-third to one-half these maxima from blue-green through yellow, declining rapidly from there through the orange and orange-red. General changes with angles of incidence as in *Morpho*, but intensities much lower.

Undersurface unremarkable, the whites being positively ultraviolet.

FAMILY PAPILIONIDAE

Papilio neophilus parianus (Huebner)

(Plate I, Figures 33(♂), 34(♀); Plate II, Figure 44(♀), right image in each frame; Plate III, Figures 51, 52(♂), second image from right in each frame; Text-figures 9e(♂), 9f(♀); Table 2).

Green spot on ♂ forewing: (Light Blue-Green of Ridgway, fading to Deep Greenish Glaucous). Ultraviolet negative, violet low; a sharp rise in blue, followed by slight maxima in the greens and in the orange.

White spot on ♀ forewing: Positively ultraviolet.

Red spot of ♀ hindwing: (Tyrian Rose to Rose Red of Ridgway, fading to Old Rose, with a distinct transparent bluish iridescent film). Ultraviolet relatively high, higher than reflectance in any other region except orange and orange-red; violet and blue moderate, blue-green and green negative; yellow-green very low; yellow low, followed by a steep rise in orange and orange-red. At large angles of incidence the effect of the short waves of the structural film is intensified, which in the ultraviolet may surpass reflectance in the orange. The iridescent sheen is more apparent in some individuals than in others.

Red spot on ♂ hindwing: As in the ♀, but a purer red, except at large angles of incidence. Ultraviolet reflectance moderately lower than in ♀, violet, blue, blue-green and green all very low to negative; yellow-green low; yellow moderately high; a sharp climb in orange and orange-red, both of which are higher than in ♀.

Pink margins of upper hindwing and pinkish dots of under wings all positively ultraviolet and unremarkable. Red body markings about as in red forewing bands of *Heliconius erato* (i.e., structural film is lacking).

Papilio anchises cymochles Doubleday

(Plate I, Figure 32; Plate III, Figures 51, 52 third (♂) and fifth (♀) image from left in each frame; Text-figure 9g (♀); Table 2)

Green and white spots of forewing in ♂ and ♀ respectively as in *P. neophilus parianus*.

Red spots on hindwings, both sexes: (Scarlet Red to Scarlet of Ridgway). Very similar to ♂ of *P. neophilus parianus* except that the ultraviolet reflectance is low, ranging from negative to about 5% in both sexes, regardless of age. There is a slight iridescent film in this species also, but the increase in ultraviolet at large angles of incidence is less pronounced than in *P. neophilus parianus*.

White margins of hindwings positively ultraviolet.

Markings of under surfaces as in *P. neophilus parianus*.

Papilio anchisiades anchisiades Esper

(Plate I, Figure 36; Plate III, Figures 51, 52, first and second images from left in each frame; Text-figure 9h (♀); Table 2)

Very similar to *P. neophilus parianus* ♂ except that red spots of hindwings (Deep Rose Pink of Ridgway fading to Old Rose) tend to a very slightly lower ultraviolet reflectance, while the values from violet through the yellow-green are slightly higher, with no negatives.

Papilio thoas neacles Rothschild & Jordan

(Plate I, Figure 35; Plate III, Figures 47-50, image at left in each frame; Text-figure 8c; Tables 2, 3)

Yellow of upper wings: (Lemon Chrome of Ridgway, fading to Straw Yellow). Ultraviolet reflectance negative; violet and blue very low to low, followed by a moderately steep climb beginning in blue-green; a near maximum is reached in the yellow, and this level continues with only a slight subsequent rise through the orange and orange-red.

FAMILY PIERIDAE

Phoebis sennae marcellina (Cramer)

(Plate I, Figure 38; Text-figures 8e (♂), 8f (♀); Table 2)

Yellow of ♂ upper wing: (Greenish Yellow to Green Yellow of Ridgway). Ultraviolet very low, about 2%, violet and blue low to moderate; a strong climb beginning in the blue-green, continuing through orange, with a drop in the orange-red.

Creamy yellow of ♀ upper wing: (Pale Ochraceous Salmon of Ridgway to Warm Buff). Differs from ♂ upper wing in much higher values in the ultraviolet, violet and blue, but lower values from the blue-green through the orange-red.

Paler lower surfaces in both sexes with moderately low and similar ultraviolet reflectances, while the reflectances in other regions also tend more towards equality.

Anteos maerula maerula (Fabricius)

(Plate I, Figure 37; Text-figure 8d (♂); Table 2)

♂ only. Greenish yellow upper wings: (Green Yellow of Ridgway). Reflectance negative in ultraviolet and violet, very low in blue; a sudden steep rise occurs in blue-green, becomes gradual in yellow-green and reaches the maximum in the orange red.

Pale undersides of wings with higher values in the short wave regions, and lower values in the long, so that the regions approach equality and show only a slight maximum in the yellow-green and yellow.

Eurema albula (Cramer), form albula

(Plate I, Figure 39; Plate III, Figure 45; Table 3)

White of upper wings in ♂ with negative ultraviolet reflectance; ♀ with up to 9% in same region. Undersurfaces reflecting up to about 5% to 8% in ♂, around 15% in ♀.

Eurema venusta (Boisduval)

(Plate I, Figure 40; Plate III, Figures 47-50, large image at right in each frame)

Table 4. Areas of Butterfly Wings Showing More Than 5% Reflectance of Magnesium Oxide at 366 mμ, Angle of Incidence 45°

(White and pale-tinted areas omitted; percentages from Table 2)

Nymphalidae	
Victorina steneles: Upper wings; green	8 %
Biblis hyperia: Upper hindwing, marginal band; red pigment with iridescent film	9 %
Callicore aurelia: a. Under forewing, except apex; red pigment with iridescent film	6 %
b. Upper forewing, band; iridescent green	12 %
Morphidae	
Morpho peleides: Upper wings; iridescent blue	16 %
Brassolidae	
Caligo illioneus: Upper hindwing; iridescent blue-violet	11 %
Papilionidae	
Papilio neophilus: Upper hindwing, spot; red pigment with iridescent film	♂, 9.5%
	♀, 14 %
Papilio anchisiades: Upper hindwing, spot; red pigment with iridescent film	♀, 8 %
Pieridae	
Phoebis sennae: a. Upper hindwing; structural and pigmentary creamy yellow	♀, 17.5%
b. Under hindwing; structural and pigmentary yellow	♂, 6 %
	♀, 7 %

♀ only. Pale yellow of upper wing surfaces reflecting about 8% ultraviolet, yellow under forewing about 7%, white under hindwing about 15%.

Melete lycimnia harti (Butler)

(Plate I, Figure 41; Table 2)

White under forewing of ♂: Ultraviolet 5%.

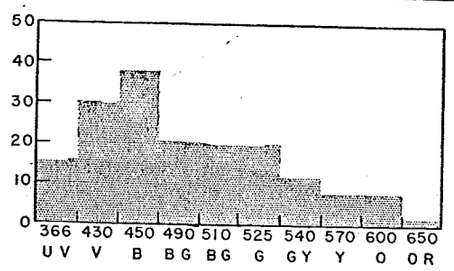
Yellow under hindwing of ♂: (Lemon Yellow of Ridgway). Ultraviolet negative, violet and blue moderately low to moderate, blue-green and green-yellow high and subequal; a steep climb in the yellow continues to rise through the orange-red.

Review of Spectral Regions

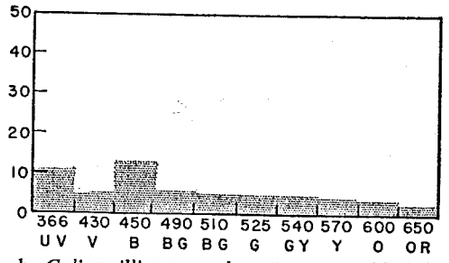
The material in the preceding systematic section will now be reviewed from the point of view of the principal spectral regions. Reference to Table 2, Text-figures 7, 8 and 9 and Plate I will be helpful in keeping the colors, spectral reflectances and appearance of the general wing patterns in mind.

A. Reflectance in the Ultraviolet Region

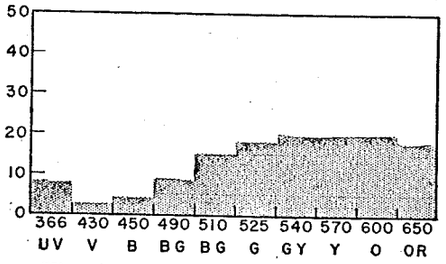
Forty-one species, belonging to 28 genera, have been surveyed in the preceding pages. Of these, only eight species show more than 5% of the reflectance of magnesium oxide at 366 mμ, in colors other than white or very pale tints. These species, all of which are included in Table 2, are listed in Table 4, along with the wing area showing the ultraviolet reflectance and its appropriate percentage at 366 mμ, when pho-



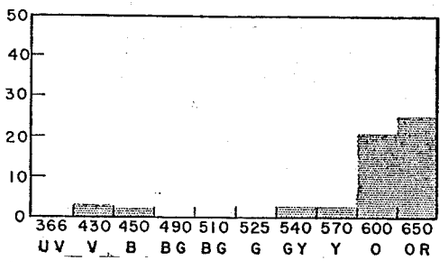
a. *Morpho peleides insularis* ♂: upper forewing, iridescent blue.



b. *Caligo illioneus saltus* ♂: upper hindwing, iridescent violet-blue.



c. *Victorina steneles steneles* ♂: upper forewing, green.



d. *Anartia amalthea amalthea* ♂: upper hindwing, red.

TEXT-FIG. 7. Reflectance characteristics of areas of special interest in selected butterflies. Typical, fresh examples illustrated. Cf. Tables 2 and 3, Text-figs. 8 and 9. Vertical coordinate, % reflectance in terms of magnesium oxide; horizontal, peak transmission of filter combinations employed, in millimicrons (see Text-fig. 4 and Table 1). Angle of incidence, 45°.

tographed with the incident light at an angle of 45°. Both sexes are similar in ultraviolet reflectance unless otherwise stated. The remaining species, reflecting less than 5% ultraviolet, have such strong reflectances in the visible that it does not seem possible that the small amount of ultraviolet could have any significant effect on the color of the area to the insect eye.

These areas of relatively high ultraviolet reflectance may be divided by their general color to human eyes, as follows:

1. *Color apparently wholly structural, i.e. highly iridescent:*
   Upper forewing green in *Callicore aurelia.*
   Upper forewing blue in *Morpho peleides.*
   Upper hindwing violet-blue in *Caligo illioneus.*
2. *Color partly structural:*
   a. A bluish iridescent film overlying a red spot or band of pigment:
      Upper hindwing margin in *Biblis hyperia.*
      Under forewing area in *Callicore aurelia.*
      Upper hindwing spot in *Papilio neophilus* (higher in ♀).
      Upper hindwing spot in *Papilio anchisiades* (♀).
   b. Structural scattering, refraction and reflection effects combined with yellow pigment:
      Upper wing creamy yellow in *Phoebis sennae* (♀).
      Under wing yellow in same species, both sexes, higher in ♀.
3. *Color apparently wholly pigmentary:*
   Upper wing green of *Victorina steneles.*

It will be seen from the above that in all except one species, *Victorina,* it is an area involving structural colors in which ultraviolet reflectance is relatively high. This species, however, also shows high reflectances in most of the remainder of the spectrum, putting it in the category of positively ultraviolet whites and pale tints, such as are commonly found on under wings where white is faintly washed with a color appearing in intense form on the upper surfaces (as in the pale pink underwing band of *Heliconius erato*). In yellow and creamy *Phoebis,* in which the color is partly structural (but non-iridescent) and

partly pigmentary, the values are much higher throughout the visible than in the ultraviolet, putting it in the usual pierid category of relatively negative ultraviolet whites and yellows.

Except in the Pieridae, white or pale tinted areas, whether wing spots, body spots, wing borders, bands or entire wings, reflect very strongly in the ultaviolet, as they do throughout the visible. In the pierids, on the other hand, ultraviolet reflectance is very low, especially in males, just as it is in white flowers (Richtmyer, 1923; Lutz, 1924; Lotmar, 1933).

The slight sexual differences found in the ultraviolet reflectances of some butterflies will be discussed below (p. 108).

Very few reflectance differences of appreciable extent emerge in the different regions of the ultraviolet. As explained on p. 95, this region was tested in three ways. First, with sunlight as the source, the photographs were made with a filter which, at the exposures used, transmitted only radiation shorter than 400 mμ; this was passed in a fairly broad arc with a maximum at 366 mμ. Second, the sun and this same filter were used in conjunction with an interference filter transmitting in a narrow band at 380 mμ. Third, a mercury vapor tube was used as a source, emitting in a narrow peak at 366 mμ, in conjunction with the usual filter to eliminate visible radiation. These three procedures gave very comparable results. In view of these checks, it seems highly unlikely that, in the species examined, there are any undiscovered bands of high ultraviolet reflectance wide enough to affect the color of the wing from the point of view of insect vision.

B. Reflectance in the Violet and Blue Regions

Most of the butterflies which are not white, pale yellow or pale green reflected very weakly in the violet and blue, the exceptions being the strongly iridescent areas of *Callicore, Morpho* and *Caligo.* In addition, the red spot of *Papilio neophilus,* particularly in the female, shows considerable reflectance in these regions.

C. Reflectance in the Blue-Green Region

Blue-green is a strong component in all butterfly colors tested except those appearing strongly orange, russet or red to the human eye; in these it is always extremely low or altogether negative. In contrast, it is strong in all yellows and their tints, in greens and in all strongly iridescent areas, although not in bluish iridescent films covering red pigments *(Callicore, Biblis, Papilio).*

D. Reflectance in the Green and Green-yellow Regions

Green and yellow-green are even more prevalent than the blue-green, being extremely weak or negative only in the purest reds, as in *Heliconius erato, H. ricini, Callicore aurelia, Anartia amalthea* and *Papilio* spp. In all the yellows, russets and oranges as well as in the strongly iridescent forms, these regions show moderate to high values, as well, of course, as in all whites and pale tints.

E. Reflectance in the Yellow Region

This region marks the beginning of the long-wave-region rise in all the reds mentioned in the preceding section except that of *Callicore,* which starts to rise only in the orange (600 mμ). For strongly yellow butterflies the maximum is not here, although reflectance is naturally high, but in the orange or orange-red, with reflectance in the green-yellow and green only slightly less than in the yellow. It is a strong component of orange and russet areas (*Dryas,* danaids, brown ithomiids, *Heliconius numata,* etc.) The iridescence of *Morpho* and *Caligo* shows a sharp falling off in the yellow.

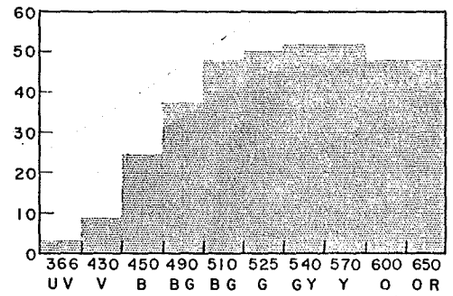
F. Reflectance in the Orange and Orange-red Regions

Practically all non-black areas in all butterflies tested show extremely high reflectance in the orange and orange-red. The exceptions are the iridescent blue and violet of *Morpho* and *Caligo.* In all the others, whether the area appears to human eyes as white, or as some form of green, yellow, orange, or red, the regions of the longest waves examined either equal or exceed those of the other regions. In areas appearing green, pale yellow-green or pale yellow the orange regions tends to be slightly higher in reflectance than the orange-red; in the purer yellows as in the orange and red areas, the orange-red component exceeds the orange in value.

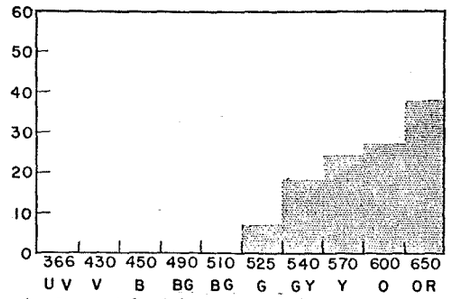
DISCUSSION AND CONCLUSIONS

The species analyzed in the preceding pages were selected on the basis of several criteria. It was desirable, first, to include varied examples of the most common local butterflies, second those with conspicuous small areas of possible signal or "recognition" value in social relationships, and finally illustrations of presumed mimicry. The group is not a systematically representative sample of Trinidad butterflies, since three families, the Lycaenidae, Erycinidae and Hesperidae, have been omitted. Nevertheless, it does comprise a generous sample of the color characteristics of typical, widely distributed neotropical species of representative colors and patterns, and so appears to furnish adequate data for a number of general observations.

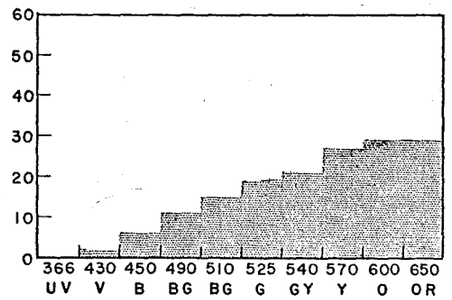
These remarks, however, are merely preliminary to analytical behavior studies on particular



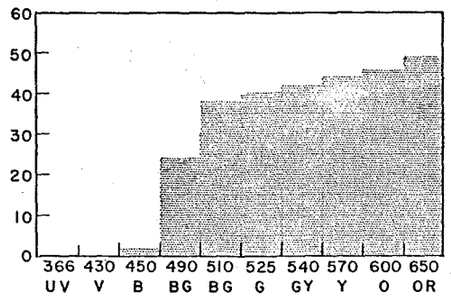
a. *Heliconius sara rhea* ♂: upper forewing, yellow spot.



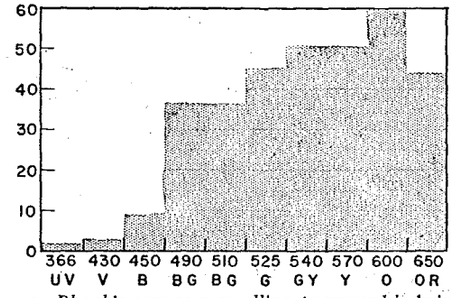
b. *Dryas julia julia* ♂: upper forewing, orange.



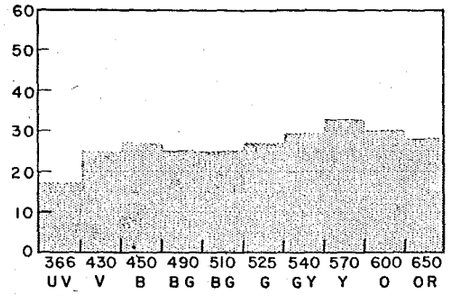
c. *Papilio thoas neacles* ♂: upper hindwing, yellow.



d. *Anteos maerula maerula* ♂: upper hindwing, yellow.



e. *Phoebis sennae marcellina* ♂: upper hindwing, yellow.



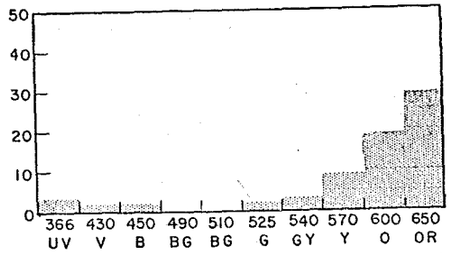
f. *Phoebis sennae marcellina* ♀: upper hindwing, yellowish.

TEXT-FIG. 8. Reflectance characteristics of areas of special interest in selected butterflies (cont.). Explanation as in Text-fig. 7.

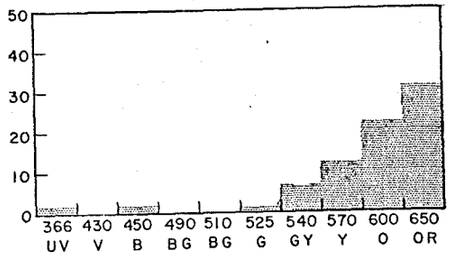
species of butterflies. Because of this, they include brief reference to experimental evidence not yet published as well as some speculative material. Both of these inclusions seem desirable in order to present an up-to-date general view of the field.

Possibilities of adaptive significance of ultraviolet reflectance in butterfly wings.—One of the primary objects of the present study was to determine whether ultraviolet reflectance from wings or body is likely to prove a widespread factor in the social behavior of the local butterflies. As has been said in the preceding section, the answer is decidedly in the negative. Excluding white and pale-tinted areas, only one-fifth of the butterflies examined had any areas reflecting more than 5% that of magnesium oxide at 366 mμ. In none of the remainder was significantly higher reflectance found between 366 and 400 mμ.

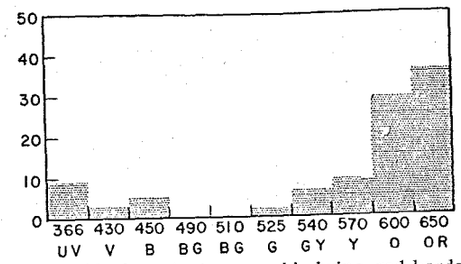
The majority, those reflecting less than 5% of ultraviolet, have such relatively strong reflectances in the visible that it does not seem possible that the low percentage of ultraviolet could, except by its subtractive effect, have any significant effect on the color of the area to the insect eye.



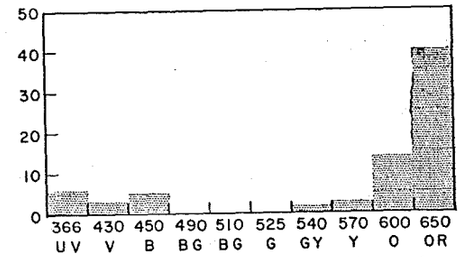
a. *Heliconius erato hydara* ♂: upper forewing, red band.



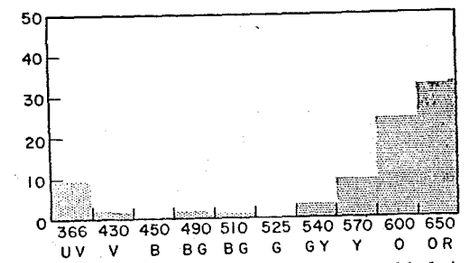
b. *Heliconius ricini insulana* ♂: upper hindwing, red area.



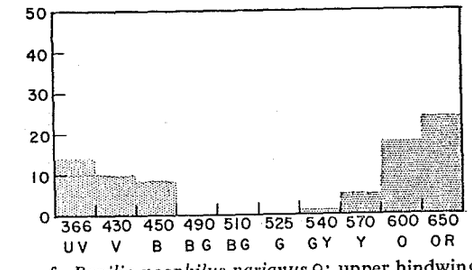
c. *Biblis hyperia* ♂: upper hindwing, red border. (Color partly structural).



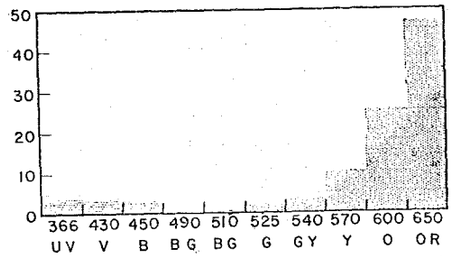
d. *Callicore aurelia* ♀: under forewing, red area. (Color partly structural).



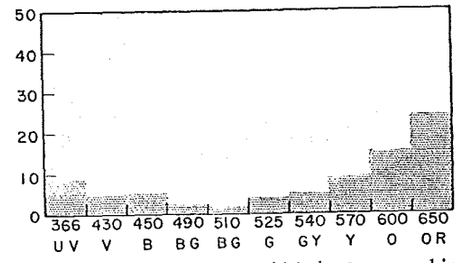
e. *Papilio neophilus parianus* ♂: upper hindwing, red spots. (Color partly structural).



f. *Papilio neophilus parianus* ♀: upper hindwing, red spots. (Color partly structural).



g. *Papilio anchises cymochles* ♀: upper hindwing, red spots. (Color partly structural).



h. *Papilio anchisiades anchisiades* ♀: upper hindwing, red spots. (Color partly structural).

TEXT-FIG. 9. Reflectance characteristics of areas of special interest in selected butterflies (cont.). Explanation as in Text-fig. 7.

This is especially true in view of the small amount of ultraviolet in sunlight reaching the earth under even ideal conditions (Text-fig. 3), which would tend to more than counter-balance the high responsiveness of insects generally to the ultraviolet (Text-fig. 2).

The question of the role played for butterflies by ultraviolet reflectance in areas appearing

white to human beings will now be considered. It seems certain that "white" for butterflies includes high reflectance in the ultraviolet between around 300 and 400 mμ, as well as in the visible, just as it does for bees (p. 89). The white areas in all families treated except the pierids reflect strongly in the ultraviolet. Therefore, they are undoubtedly "true" whites for the butterflies, since current experiments (in ms.) show first, that butterflies of all families included in this study are unquestionably highly sensitive to the ultraviolet, and, second, that at least in the Heliconiidae, negatively ultraviolet white is distinguished from positively ultraviolet white, and is treated by them as a color. It is also attractive to them under certain conditions, exactly as it is in bees. Also as in bees, positively ultraviolet white is never attractive or, apparently, particularly conspicuous to them. This may very likely be because of the prevalence of highly reflectant, unimportant surfaces, such as wet leaves, in their natural environment.

However that may be, it seems that ultraviolet reflectance from white wing areas can be of adaptive importance to butterfly social behavior in only two ways. The first would be as part of a distinctive pattern, such as in *Phyciodes, Dynamine* or *Adelpha.* Nothing is as yet known of this aspect. Second, in the pierids only, it might be significant by its absence. As has long been known, a low ultraviolet reflectance is a characteristic of the pterines which are largely responsible for the whites and yellows in this family (review in Timon-David, 1947). Ilse (1928; review 1941) found that *Pieris rapae* Linnaeus responded with courting behavior to yellowish-white paper models. At that time, however, she was not taking possible ultraviolet reflectance into consideration, it being then undetermined that pierids were sensitive to that region. If pierid color vision proves after all to be basically similar to that of bees and other butterflies, it would be a negatively ultraviolet white, an approach to bee-blue-green, to which they would respond in courting. However Ilse (1937; review 1941) has assembled strong indirect evidence that, for pierids, ultraviolet is not complementary to the blue-green-to-green region which they distinguish apart from blue and yellow (see p. 89). According to her experiments with egg-laying responses, "red, mauve and violet" are all treated as complementaries to green, which would seem to preclude ultraviolet in that role. The entire problem remains one of particular interest.

In 1952 Makino and his co-workers reported on the higher ultraviolet reflectance in female *Pieris rapae* compared with males, and gave the chemical characteristics responsible for the difference. These authors did not, however, report the degree of difference, or the amount of reflectance relative to a standard. In the present study, sexual differences in ultraviolet reflectance have also been found to be characteristic of all the pierid whites and yellows tested, as well as of the browns and russets of danaids and ithomiids. In all of these the ultraviolet reflectance is low —in the browns less than 4% on the upper sides in both sexes, and in the white and yellow pierids less than 5%, at least in the males. The greatest sexual difference was found in *Phoebis sennae,* in which the yellow male reflects about 2% and the pale, cream-colored female 17% or more from the upper wing surfaces. According to Hertz's experiments with bees (1937, 1939), it is necessary for a white paper to reflect more than a third in the ultraviolet of the level of the general reflectance in the visible in order to be treated as "white"—i.e., uncolored—by bees; if the relative reflectance in the ultraviolet is as low as one-fourth the level in the visible, it will be treated, in sunlight, as colored by bees—as equivalent, that is, to bee-blue-green. In the pierids, which are so highly reflectant in the visible, the increased reflectance in the ultraviolet appears to be rarely if ever enough to render the females uncolored to the males; presumably, however, the males would appear a purer hue than the females. Work on this problem remains to be done.

The pale green of *Victorina,* although it has rather high reflectance in the ultraviolet, reflects so strongly throughout most of the visible that it seems unlikely that the ultraviolet can affect its hue for butterflies except to render it more nearly white (uncolored).

The possibilities of adaptive significance of ultraviolet reflectances have now been considered and largely discounted in all except one small group. This includes those butterflies with iridescent areas on the wings (Table 4). These six species—a *Callicore,* a *Biblis,* a *Morpho,* a *Caligo* and two *Papilio*—alone of those analyzed seem likely to have evolved a connection between their ultraviolet reflectance and their social behavior. All of these systematically scattered forms have employed similar means, through structural colors (presumably of the interference type), of producing ultraviolet.

In the upper wings of *Morpho* and *Caligo* and the upper wing-bar of *Callicore,* interference colors are entirely responsible (excluding the usual dark pigmented bases to the laminated scale plates). In the remaining species, the under forewing of *Callicore,* the upper hindwing margin of *Biblis* and the upper hindwing spots of *Papilio,* a delicate, bluish iridescent film overlies a vivid red pigment. This film is invisible to the human eye except at large angles of incident light.

In all of these iridescent effects, whether or not red pigment is also involved, the operation of the usual laws governing interference colors is very evident (see e.g., Richards, 1951, p. 197 ff., and Fox, 1953, p. 56 ff.). Briefly, and excluding variable side effects such as surface scattering of light by both fine and macroscopic irregularities, the smaller the angle of incidence, the longer the wavelengths of the region of highest intensity. As an example, a well-flattened small piece of *Morpho* wing, viewed directly in line with the light (that is, at a 0° angle) will appear blue-green to the human eye, at a 45° angle it will appear blue, and, finally at increased angles of incidence the highest relative ultraviolet values are recorded by photographic means.

However, in *Morpho* at least, because of the details of number, order, intervening distances and varying thickness of the superimposed plates, the highest absolute intensities occur when the wing is illuminated at the smaller angles of incidence (Anderson & Richards, 1942); at these angles ultraviolet values are at a minimum.

Now, the possible significance of these iridescent areas in intraspecific behavior may be as follows: With every wingbeat, a flying *Morpho* butterfly changes the angle of light incidence through the entire possible range. To the human eye, a *Morpho* in flight is simply a flickering flash of varying tints of blue. However, to another *Morpho,* in sunlight, there should be a brilliant shift from blue-green or blue to ultraviolet, then momentary extinction and back again through the spectral arc; conceivably this may be an exceptionally potent stimulus. The well-known dipping of these butterflies to blue papers and other objects suggests strongly that the wing color may prove to be a sign stimulus in inter-male or courtship behavior.

The delicate iridescent sheen of the red band of *Biblis,* and of the red spots of *Papilio* is invisible on the wing to human beings. Nevertheless, as in *Morpho,* it seems likely that these areas may prove to be of adaptive importance, the blue-to-ultraviolet effect, as in the strongly iridescent butterflies, being perhaps visible during flight, or when the wings are open and shut, in the characteristic motion of butterflies at rest. If so, it seems possible that the presumed aposematic coloring of *P. neophilus* and its mimic, *P. anchisiades,* may have a double function. The visibility of the iridescent red areas in both *Biblis* and *Papilio* may be strongly enhanced for insect vision by the breaking up of the red by means of the fine black cross-bars (see responses of butterflies and bees to form, Ilse, 1932.2; von Frisch, 1950).

The subdued iridescence of *Caligo illioneus* follows, in lower key, the same laws as the others, and to the insect eye the butterfly might well, in full sunlight, give a moderately strong blue-to-ultraviolet flash. However, this species flies only at twilight and only among trees, where ultraviolet is a negligible component of the feeble light. Therefore an adaptive use of its reflectance pattern in intraspecific behavior seems to be extremely unlikely in this species. Possibly the iridescence is here a vestigial character. Experimental work on these problems is in progress.

Reflectance in the Visible.—The major characteristic here is that the occurrence of reflectance is progressively higher toward the long wave end of the spectrum. Violet and blue are rare and scanty spectral components—except in structural colors where they are the rule. Blue-green is a strong component except in brown, russet, orange or red, while the various greens are weak or negative only in the orange-reds and reds. Yellow, orange and red are the most prevalent of all, being strong components of practically all butterfly pigments. In the present group, in fact, they are weak only in the spectra of the entirely structurally colored areas of *Morpho* and *Caligo.* This is altogether in accordance with the absorption spectra of various prevalent insect pigments, including carotenes, anthoxanthins and some pterins, in which violets and blues are largely absorbed (reviews in Timon-David, 1947; Karrer & Jucker, 1950; Fox, 1953).

An important point in connection with butterfly red is this, that all reds—whether in butterflies or in flowers—reflect highly in the orange as well, and often show also considerable amounts of yellow. Even if butterflies prove to be as weakly sensitive to wavelengths longer than 650 mμ as bees and other insects (p. 88, Text-figs. 1, 2), they would still be able to perceive with ease the yellow and orange components of the area— whether as one or more distinct hues is, at the moment, immaterial. Thus the well-known predilection of pierids and papilionids for red flowers in feeding (Ilse, 1928; Kaye, 1921, and present author's observations) may well be due to an attraction or extra sensitivity to the orange components, rather than to an extension of their spectral range at an efficient level into the red.

Results of Fading.—It is well known that the pigments of many butterflies fade considerably even in life; this is especially true locally of *Heliconius erato, Anartia amalthea* and *Victorina steneles.* In every case the results from the point of view of reflectance patterns are, for

the reds, higher reflectance (i.e., reduced absorption) in the orange and yellow. Similarly, in visually green areas, faded specimens show higher reflectance in the shorter wave regions, while the long wave reflectance is practically unchanged.

No significant difference in reflectance patterns was found between specimens freshly killed before photographing and those which had been dried, providing only that the specimens had been protected from light and rubbing. The use of chloroform or paradichlorobenzene had no observable effect on the reflectance results.

Conclusions.—The following statements, outside the realm of speculation, may now be made concerning the reflectance of the butterfly wing patterns analyzed, and in regard to the possible adaptive significance of the ultraviolet in intraspecific behavior.

1. In only five species out of 41 is ultraviolet reflectance at all likely to be involved adaptively in their social behavior. This is in the blue of *Morpho,* in the red hindwing border of *Biblis,* under forewing red of *Callicore* and the hindwing red spots of *Papilio neophilus* and *P. anchisiades,* both of the latter primarily in the female. In all of these species the colors are altogether or partly structural.

2. Except for the positively ultraviolet red areas mentioned, no unexpected areas of possible intraspecific signal or stimulating value were discovered. All blacks proved to be negatively ultraviolet; ocelli on the underwings of *Euptychia, Morpho* and *Caligo* were composed simply of minus-ultraviolet browns and russets and positively ultraviolet whites; neither cryptically colored areas, so prevalent on the underwings, nor the striking combinations of reds (except those previously noted), oranges, yellows, browns, blacks and whites of presumed aposematic coloring, and of Batesian or Mullerian mimicry, showed any unusual or unexpected spectral characteristics whatsoever. In other words, none of the reflectance patterns showed any hidden spectral components in the ultraviolet which might be interpreted as special adaptions to insect vision, rather than only to the vision of vertebrate enemies (see Cott, 1940; Goldschmidt, 1945; and Allee *et al.,* 1949, p. 669 ff., for recent reviews and comment on this still contentious subject).

3. All of this is in accordance with the conclusions of Lutz (1924) and Weiss (1945, 1946) on the apparent lack of correlation between the sensitivity of insects to the ultraviolet and the amount of ultraviolet either in their environment in general or reflected from the flowers which they pollinate.

In fact, it appears increasingly obvious that ultraviolet sensitivity is a mere byproduct of the physiological processes of the insect eye. The chemical steps in the formation and destruction of photosensitive pigments in insects have still to be worked out. Nevertheless, it is already known that the primary photosensitive substance in the insect retina has an absorption curve practically identical with that of rhodopsin in man (Roeder, 1953, pp. 515 ff. and ref. See also Prosser, 1950, pp. 408, 410-411, 422 ff. and ref. for related subjects). However, unlike the vertebrate eye, in which ultraviolet is largely absorbed before reaching the retina, this short-wave region is unimpeded by the outer elements of the insect ommatidium.

In brief, it appears from the present study that only rarely has any correlated evolution of wing color occurred in response to this ultraviolet sensitivity which could be of possible significance in intraspecific relations, and that in the few potential examples, the ultraviolet role is played by structural rather than pigmentary colors.

4. The high reflectance in the orange of all red butterfly pigments would theoretically make these "reds" of usable brightness to the insects, even though they prove to have, as do other orders of insects, negligible visual sensitivity around and above 650 mμ.

Conclusions on the adaptive value of color and pattern in the visible, and of the juxtaposition of hues, in intraspecific behavior must await the completion of forthcoming studies.

Summary

1. A method is described of determining the spectral composition of the colors of butterfly wings. The technique employs photography through combinations of narrow band pass and interference filters with peak transmissions ranging from 366 to 650 mμ. A scale of standards, of known spectrophotometric reflectance in terms of magnesium oxide, is included in each negative. Negative images are subsequently analyzed with a densitometer, their densities being compared with the standards in each frame. By this means preliminary analyses of entire wings were carried out, as well as detailed examinations of highly magnified areas of special interest.

2. Forty-one species of Trinidad butterflies belonging to 28 genera were thus analyzed as a prerequisite to studies of the adaptive value of color, including the ultraviolet, in intraspecific behavior.

3. Only eight of these species show any areas other than white and pale tints having more than 5% reflectance in the ultraviolet. The colors of all of these areas are either partly or altogether structural in nature. In only five of these species is it considered at all likely that these special areas, all more or less iridescent, would prove to be of adaptive value in intraspecific behavior.

4. Spectral characteristics in the visible are unsurprising, with a preponderance of reflectance in the long wave regions, regardless of apparent hue. Examples of presumed Batesian and Mullerian mimicry show similar spectral patterns, all with minimal ultraviolet reflectances. It is pointed out that the high reflectance of all reds in the orange region would make these pigments of adequate visibility even to insects for which the visible spectrum may be curtailed beyond the orange-red.

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EXPLANATION OF THE PLATES

PLATE I

Species and subspecies of butterflies used in color analyses. Not all the specimens appearing in this plate were captured in Trinidad; therefore size ratios are not always typical of the island populations. All species, or their close relatives, are illustrated in color in Seitz: Macrolepidoptera of the World; The American Rhopalocera, Vol. V, Plates. (1924).

FIG. 1. *Danaus plexippus megalippe.*
FIG. 2. *Lycorea ceres ceres.*
FIG. 3. *Tithorea mopsa megara.*
FIG. 4. *Mechanitis doryssus veritabilis.*
FIG. 5. *Hypothyris euclea euclea.*
FIG. 6. *Hypoleria ocalea.*
FIG. 7. *Ithomia drymo pellucida.*
FIG. 8. *Hymenitis andromica trifenestra.*
FIG. 9. *Euptychia hermes hermes.*
FIG. 10. *Euptychia hesione.*
FIG. 11. *Heliconius numata ethilla.*
FIG. 12. *Heliconius erato hydara.*
FIG. 13. *Heliconius sara rhea.*
FIG. 14. *Heliconius ricini insulana.*
FIG. 15. *Heliconius aliphera aliphera.*
FIG. 16. *Dryas julia julia.*
FIG. 17. *Agraulis vanillae vanillae.*
FIG. 18. *Phyciodes ofella ofella.*
FIG. 19. *Phyciodes leucodesma.*
FIG. 20. *Anartia amalthea amalthea.*
FIG. 21. *Victorina steneles steneles.*
FIG. 22. *Biblis hyperia.*
FIG. 23. *Callicore aurelia.*
FIG. 24. *Colobura dirce dirce.*
FIG. 25. *Dynamine theseus.*
FIG. 26. *Dynamine artemesia.*
FIG. 27. *Adelpha iphicla daceleia.*
FIG. 28. *Adelpha cytherea insularis.*
FIG. 29. *Protogonius hippona trinitatis.*
FIG. 30. *Morpho peleides insularis.*
FIG. 31. *Caligo illioneus saltus.*
FIG. 32. *Papilio anchises cymochles* ♀.
FIG. 33. *Papilio neophilus parianus* ♂.
FIG. 34. *Papilio neophilus parianus* ♀.
FIG. 35. *Papilio thoas neacles.*
FIG. 36. *Papilio anchisiades anchisiades* ♂.
FIG. 37. *Anteos maerula maerula.*
FIG. 38. *Phoebis sennae marcellina.*
FIG. 39. *Eurema albula* f. *albula.*
FIG. 40. *Eurema venusta.*
FIG. 41. *Melete lycimnia harti.*

PLATE II

Preliminary surveys of spectral characteristics of butterflies: Sample negative film strips photographed through only six filter combinations. Entire butterflies are shown, along with knife blade coated with magnesium oxide and used as a rough standard. Each film strip includes, from left to right, frames covering roughly the six following regions: ultraviolet (peak transmission at 366 mμ), violet-blue (peak at 430 mμ), blue-green (peak at 510 mμ), green-yellow (peak at 540 mμ), yellow (peak at 570 mμ), orange-red (peak at 640 ff.). For complete explanation, see text, p. 91 ff.

FIG. 42. In each frame, from left to right: *Callicore aurelia,* right under side; *Adelpha iphicla daceleia,* upper; *A. cytherea insularis,* upper.

FIG. 43. In each frame, upper sides: left, *Heliconius numata ethilla;* right, *Tithorea mopsa megara.*

FIG. 44. In each frame, from left to right, upper sides: *Heliconius aliphera aliphera; Agraulis vanillae vanillae; Papilio neophilus parianus* ♀. (Positions of frames 11 and 12 are transposed in the reproduction since, in exposing these two negatives, the respective filter combinations were inadvertently used in transposed order).

PLATE III

FIG. 45. Negative illustrating arrangement of butterfly wings and standards in photography by sunlight with ultraviolet filter. The four vertical pairs of images in central portion of negative are the white wings of a pierid, *Eurema albula,* arranged as follows from left to right; under wings, ♀; upper wings, ♀; under wings, ♂; upper wings, ♂. The 19 steps of gray standards are placed, in two strips, above and below wings; colored standards of high ultraviolet reflectance are in vertical strip near right edge of negative. Note minimum ultraviolet reflectance of upper wings in ♂. The unevenness of density in images of individual wings is a typical result of sunlight photography of colors due partly to structure rather than almost entirely to pigment, and illustrate the care needed in analysis with the densitometer; see p. 96.

FIG. 46. Negative illustrating arrangement of small pieces of butterfly wings and standards in photography by sunlight with ultraviolet and interference filters, giving a narrow peak transmission at 380 mμ. The six central images are pieces cut from the red pigmented forewing bands of individual *Heliconius erato hydara,* representing both sexes and various ages. Gray standards placed as in Fig. 45; colored standards near left edge of negative.

FIG. 47. Negative illustrating arrangement of wing pieces and standards in photography indoors by ultraviolet lamp and ultraviolet filter. Five central images, from left to right, *Papilio thoas neacles,* upper hindwing yellow with black margins (practically negatively ultraviolet and therefore invisible in reproduction); *Heliconius sara rhea,* upper forewing, yellow spot surrounded by black; *Heliconius ricini insulana,* upper forewing, yellow spot surrounded by black; *Eurema venusta,* ♀, under forewing, yellow; same, under hindwing, whitish. (See Figs. 48-50 for same group photographed through other filter combinations). Colored and gray standards (darker half) in two strips, above and below images, respectively. Note low reflectance, indicated by low negative density, of all specimens except *Eurema.*

FIG. 48. Same specimens, photographed by photoflood lamp through filters with a peak transmission in the violet-blue (430 mμ). Only darker half of gray standards is included.

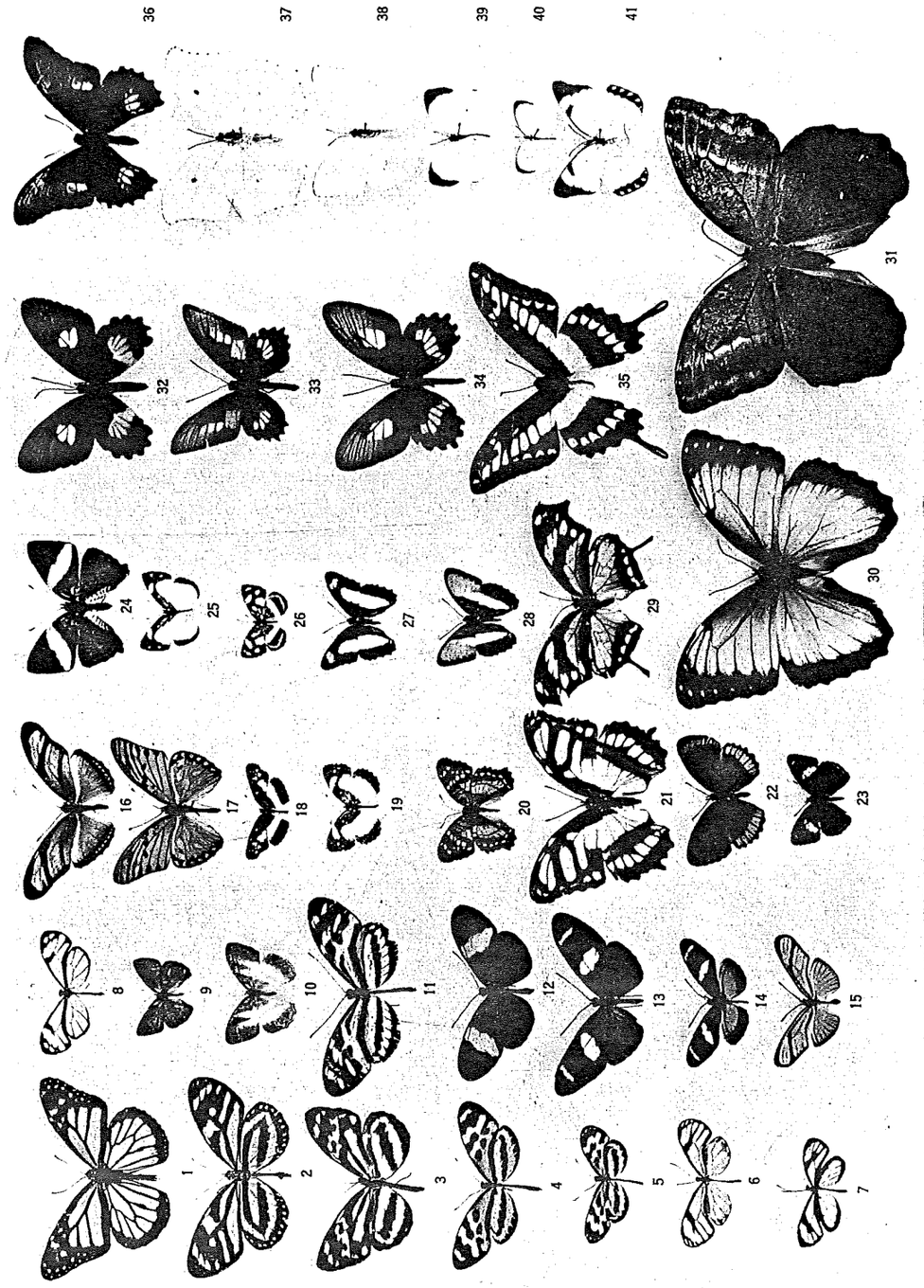
FIG. 49. Same specimens, photographed by photoflood lamp through filters with a peak transmission in the orange (600 mμ). Only lighter half of gray standards is included. Note high reflectance indicated by high negative density, of all specimens here and in Fig. 50.

FIG. 50. Same specimens, photographed by photoflood lamp through filters with a peak transmission in the orange-red (650 mμ). Only lighter half of gray standards is included.

FIG. 51. Red hindwing patches of *Papilio* spp., photographed by photoflood lamp through filters with a peak transmission in the orange (600 mμ). Only lighter half of gray standards is included. From left to right: *Papilio anchisiades anchisiades,* ♂; same, ♀; *P. anchises cymochles,* ♂ (piece of spot only); *P. neophilus parianus,* ♂; *P. anchises cymochles,* ♀.

FIG. 52. Same, photographed through filters with a peak transmission in the orange-red (650 mμ).

FIG. 53. Arrangement of camera, stand and lights for indoor photographic analysis of butterfly colors.



SPECTRAL REFLECTANCE CHARACTERISTICS OF BUTTERFLIES
(LEPIDOPTERA) FROM TRINIDAD, B.W.I.

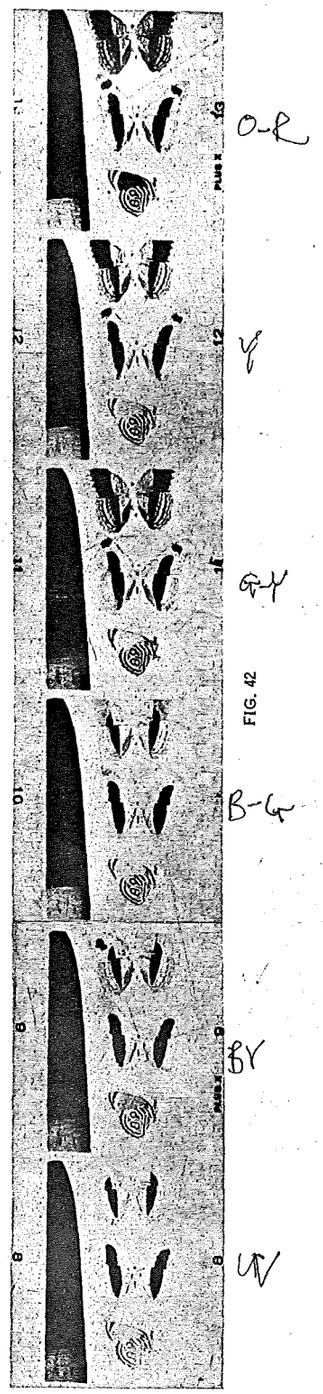


FIG. 42

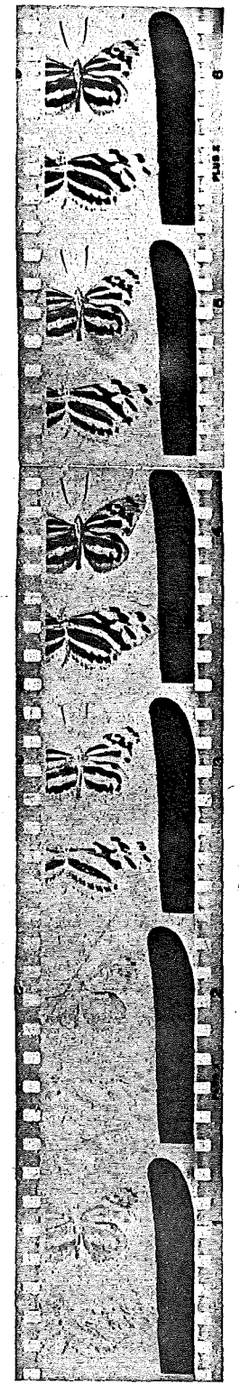


FIG. 43

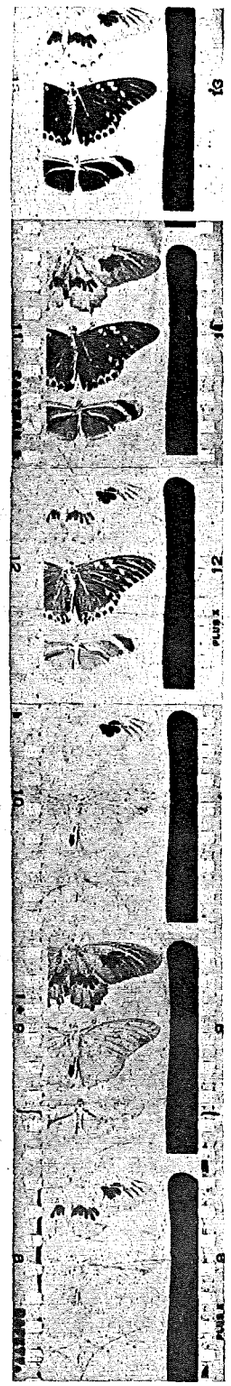


FIG. 44

SPECTRAL REFLECTANCE CHARACTERISTICS OF BUTTERFLIES
(LEPIDOPTERA) FROM TRINIDAD, B.W.I.

FIG. 51

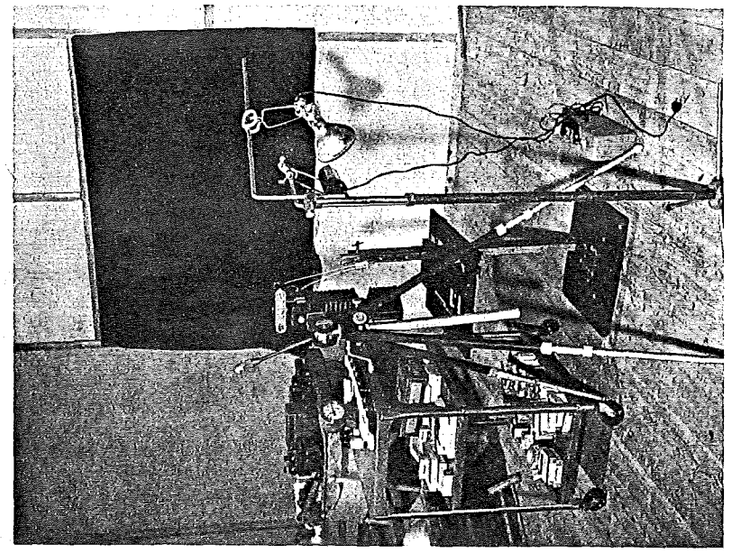


FIG. 52

FIG. 53

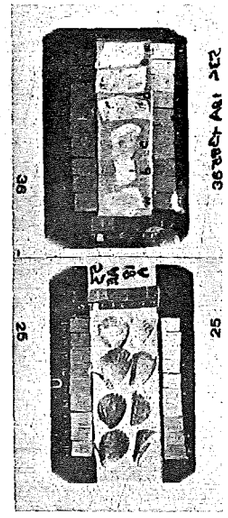


FIG. 45

FIG. 46

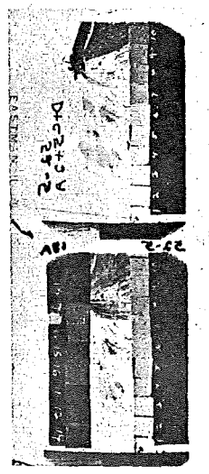


FIG. 47

FIG. 48

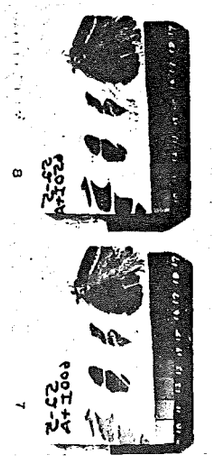


FIG. 49

FIG. 50

SPECTRAL REFLECTANCE CHARACTERISTICS OF BUTTERFLIES
(LEPIDOPTERA) FROM TRINIDAD, B.W.I.