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OBSERVATIONS ON THE DEVELOPMENT OF COLOR
IN THE
PUPAL WINGS OF SEVERAL SPECIES OF LITHOCOLLETIS.

A THESIS

by

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Submitted to the Faculty of the
Graduate School
of the
University of Cincinnati

In partial fulfillment of the requirements for the
Degree of
Doctor of Philosophy.

UMI Number: DP16661

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OBSERVATIONS ON THE DEVELOPMENT OF COLOR
IN THE
PUPAL WINGS OF SEVERAL SPECIES OF LITHOCOLLETIS.

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I. Introduction.

Studies upon the development of color and color pattern in insects have been undertaken for two purposes, first, to determine the origin of the pigment-forming material and the processes which change it into the adult colors, and second, to observe the changes, if any, which take place in the form of the color areas themselves, bringing about their transformation into the adult color patterns.

Whereever studies of this character have been made upon the pupal wings of Lepidoptera, the observations have been almost entirely confined to the Macrolepidoptera. The Microlepidoptera, which are a more primitive group, and therefore may be expected to give more direct evidence of the steps in the evolution of the color pattern, have been almost neglected. Within this group, abundant and excellent material for such a study is afforded by the species of the genus *Lithocolletis*.

The observations upon the development of color in the wings of *Lithocolletis*, presented in this paper, were made with the object of ascertaining the primitive color pattern.

It is a pleasure to express my appreciation to Dr. M. F. Guyer for his many helpful suggestions during my work.

II. Historical.

Tower ('06) has summarized the general results of researches upon the development of colors in pupal wings as follows:

"The studies upon the origin of color in the wings of Lepidoptera have shown that there is a regular order of development, not only of colors, but also of the areas in which spots and stripes appear. The wings, which are colorless at first, become opaque, yellowish or light drab, beginning first near the base, of the wing and spreading distalward. Soon spots, stripes, and adult markings appear, at first proximal, then more and more distal, then between the nervules, and, last of all, upon the nervules. First the purely pigmental colors develop, and these are followed by the chemico-physical."

The principal researches have been those by Schäffer ('82) Van Bemmelen ('89), Urech ('91), Haase ('93), Mayer ('96), and most recently by von Linden ('98, '02). The principal work of the first three authors was upon *Vanessa* and *Pyrameis*. Van Bemmelen ('89) has shown that the first color to appear in *Pyrameis cardui* is a pale brownish yellow which deepens to the reddish brown ground color; upon this ground color the black spots appear. The development of the color in *Vanessa urticae* follows very much the same sequence, as pointed out

by both Van Bemmelen and Urech. Urech ('91) has shown that in *Vanessa io*, the adult spots and colors appear directly upon the primitive white of the pupal wing; that is, the yellow appears over a restricted area of the wing; following this a reddish tinge appears, which, over another portion of the wing gradually deepens to the reddish brown ground color; later, the adult black spots develop directly upon the primitive white wing; some at least of the white spots of the adult represent the primitive white of the pupal wing. In Van Bemmelen's opinion, a considerable amount of modification takes place in the wings after the first appearance of color, so that the adult design may differ considerably from that first laid down. Urech's ('91) view is directly opposed to this; according to him, the different color areas are definitely laid down from the beginning, and are therefore older phylogenetically than the particular colors of the adult wing. He therefore regards color as the important factor in determining phylogenetic position -- "die Farbe ist das Primäre, die Zeichnung das Secundäre".

Haase ('93) worked upon several species of *Papilio* and found that the wings are transparent or colorless, later becoming whitish; this white then gives way to a yellowish ground color upon which the adult colors begin to appear, undergoing considerable development before reaching their definitive adult condition.

Mayer ('96) traces the development of the scales from modified hypodermis cells, the "formative cells of the scales", from their first appearance as blunt outgrowths from these cells until they are fully formed and pigmented. In addition to confirming the conclusions of previous investigators as to the sequence in the appearance of colors, Mayer has shown that "the transparent condition of the wings corresponds to the period before the scales are formed, and to the time when they are still completely full of protoplasm. The white condition is caused by the withdrawal of the protoplasm from the scales, leaving them as little hollow bags filled with air. In this condition they diffract the light and appear pure white."

"After the protoplasm has completely withdrawn from the scales, the 'blood' or haemolymph of the pupa enters them, and soon after this, the wing becomes of a uniform dull yellow or light drab color. This color is due to the fact that soon after the haemolymph has entered the scales it changes to a dull ochre-yellow, and finally to a drab color. The same change takes place in haemolymph which has been removed from the pupa and exposed to the air. The mature colors are due to chemical changes in the haemolymph itself. They first appear in places between the nervures, never upon the nervures themselves. The last places to acquire the mature coloration are the outer and costal edges of the wings and the nervures.* *"

"Dull ochre-yellow and drabs are, phylogenetically

speaking, the oldest pigmental colors in the Lepidoptera; for these are the colors that are assumed by the haemolymph upon mere exposure to air. The more brilliant pigmental colors, such as bright yellows, reds, greens, etc., are derived by more complex chemical processes. We find that dull ochre-yellows and drabs are at the present day the prevalent colors among the less differentiated nocturnal moths. The diurnal forms of Lepidoptera have almost a monopoly of the brilliant colorations, but even in these diurnal forms one finds that dull yellow or drab colors are still quite common upon those parts of their wings that are hidden from view."

The most recent researches upon the subject of development of color in the pupal wings of Lepidoptera are those of von Linden ('98, '02). The results of her investigations are embodied in two papers, the first being practically included in the second. Her observations lead to the conclusion that the adult color-pattern develops from a number of separate transverse bands which dispose themselves upon a uniform ground color in a manner characteristic of each species. A distinction is thus made between ground color and that forming the color pattern. These transverse bands (longitudinal according to Eimer's view) occupy definite positions upon the wing determined by the course of the nervures and tracheae. This is the condition found among Papilios

Vanessas, Sphingids, the higher Bombycids and even among some of the Geometrids. These larger bands are formed by the broadening out and fusion of narrower bands ("bandelettes primaires") preserved only among more primitive forms. On the one hand, the bands may fuse to form a uniform color; on the other, they may break up into a series of spots, which become smaller as the ground color encroaches upon them. The hindwing is arrested at a point less advanced than the forewing; this, combined with the greater tendency toward fusion of the bands which is in fact due to the modified form of the hindwing, creates the erroneous impression that the hindwing is more advanced than the forewing.

The author claims that her results support the laws which Eimer has promulgated for species differentiation based upon a study of adult coloration.

"Il est donc évident que les lois que Eimer a trouvées en étudiant la phylogénèse du dessin des Lépidoptères peuvent être admises point pour point pour l'ontogénèse."

"Mes recherches prouvent donc que les dessin des Papillons ne paraît pas soudainement, * * * * que les phases que ce dessin parcourt pendant son développement ontogénétique, sont analogues aux phases que le dessin de l'espèce du Papillon a dû parcourir pendant son développement phylogénétique, que le loi qui gouverne la biogénèse est aussi confirmée par ce procédé, qui s'accomplit pendant la métamorphose de l'insecte,

et qu'en fin les théories de Eimer sont solidement fondées, quand il dit que chaque animal ne peut varier que dans peu de directions déterminées par les influences du dehors et par sa propre constitution, et que l'espèce se forme par génépiastase."

Recapitulation is however only partial and confined to primitive forms:

"Les phénomènes de la phylogénèse se produisent le plus clairement dans le développement du dessin chez les formes les plus primitives. Chez les groupes les plus avancés, ces phénomènes sont masqués par l'intervention de la tachygenèse, qui montre sa plus grande influence dans le développement des ailes inférieures."

With regard to the succession of colors upon the wing the same author finds that it is only in the primitive forms that the scales forming the dark markings pass through the intermediate shades of yellow to reach their final gray or black condition; in the higher forms they remain uncolored until the scales forming the ground color reach their full development, later passing directly from the colorless stage into gray or black. The color appears first at the tip of the scales, spreading gradually to the base. Scales which are destined to acquire their pigment later are not fully formed when the scales of the ground color attain the adult form and color. Therefore, color may be taken as a measure of the degree of development of a scale.

III. Methods and Observations.

a. Methods.

In the study of the development of color in the wings of *Lithocolletis*, specimens of the summer generations were used for observation. No overwintering pupae have been observed. In the summer generations, the average duration of the pupal state is about a week; it may be as short as four or five days.

The chrysalids were removed from the mines shortly after pupation and kept under careful observation. For some time no change in the brown color of the pupa is to be observed, then two faintly darker brown spots, corresponding in position with the eyes of the imago, become visible through the pupal envelope.. These spots rapidly turn black, and very shortly after, the wings, which up to this time have appeared transparent through their thin chitinous envelope, begin to lose their transparency. This marks the beginning of the white stage. A day or two later the yellow colors begin to appear upon the wing. The chief difficulty in the study lies in securing a suitable series of these earliest stages, as the colors are very faint at this period, and numerous dissections are often required before the necessary material can be obtained. In later stages, the markings are visible through the pupal envelope, and a choice of specimens can be made

with relative accuracy.

The dissections were made in .6% NaCl solution under a simple dissecting microscope of moderate power, by means of fine needles set in match-sticks. One needle is inserted through the abdomen and held rigid; another through the middle of the upper side of the thorax. The second needle is then drawn forward, tearing apart the pupal envelope and carrying with it the anterior part of the thorax with wings attached. The structure of the pupa with separate envelopes for wings and legs in the lower Microlepidoptera renders this method of procedure highly successful. The thorax may now be torn apart, allowing the wings to float out flat. With a little experience, it is possible to remove the wings in this manner without the displacement of either scales or cilia. The wings thus removed from the pupa, vary in length from 1.5 to 2 mm., being therefore about one-half the length of the imaginal wings.

The wings were examined with a simple lens to determine the general extent of the color areas. For the more accurate observation of the positions and limits of pigmented areas, and individual scales pigmented, I have used a compound microscope, 16 mm. objective, 4x eyepiece, giving a magnification of 60 diameters. The observations were made almost entirely by reflected light, and under a cover glass. In the early stages, where the colors are very faint, I have

found black paper, as suggested by von Linden, very useful for a background. Somewhat later, a pure white background is advantageous in the detection of the first appearance of grayish tints.

All of the wings were examined in .6% NaCl solution, shortly after removal from the pupa. Observations made thus are vastly more satisfactory than when permanent mounts are employed. A number of the wings were however transferred to absolute alcohol between pieces of glass to prevent curling, and after about an hour embedded in Venetian turpentine made as follows:

Commercial Venice turpentine is mixed in a tall cylinder glass with an equal volume of 95% alcohol. The mixture is allowed to stand in a warm place for three or four weeks and then decanted.

The mounting medium thus prepared is thin enough to flow easily and not displace the delicate cilia. However, the attendant darkening of the colors is a disadvantage in comparing with adult specimens.

I have found it possible to preserve all except the earliest stages without the use of a mounting fluid, if the slide containing the wing under a cover glass is immersed in absolute alcohol for a short period. Later the cover glass may be closely appressed and fastened down around its edges.

Both forewings in each specimen were examined; the

two sets of observations thus serving as a check on one another. In the following descriptions reference is made to the forewings only. The hindwings are practically unicolorous, usually paler than the forewings, and reach their final development somewhat in advance of the forewings. Their development yields no new facts, merely confirming the results of earlier investigators upon the sequence of colors.

b. Observations on the Development of Color in the Pupal Wings.

Two factors were taken into consideration in determining the choice of species to be studied, namely, the general type of adult marking, and the presence of certain characters such as an apical spot or dark marginings adjacent to white streaks or fasciae. The object of the research is two-fold, (1) to determine, if possible, the primitive or fundamental color pattern and its mode of transformation into the adult pattern, (2) to determine the relative time of appearance and manner of development of the various dark markings, the characters referred to above.

The evidence furnished by the development of color in the pupal wings taken in conjunction with a comparative study of the adult markings (to be presented elsewhere) has convinced me that the primitive color pattern is composed of a series of uniformly colored pale yellow bands, seven in number, placed transversely on the wing and separated from one another by white fasciae (unpigmented areas) (Fig. 1). These bands are typically straight, and, with the exception of the first, cross the wing almost perpendicular to the margins. The bands when present in their primitive condition, have certain defined positions. Their hypothetical typical positions are illustrated by Fig. 1. In what follows it will be noticed that there is a definite relation of bands to veins. Band I occupies the extreme base of the wing, beginning at the base

of the dorsum and broadening on the costa; the white streak which separates it from Band II passes obliquely from the base of the dorsum toward the costa, lying over the point of origin of the tubular portion of the lower median vein. Band II crosses the wing on the basal side of vein 12; the position of the white fascia which separates it from Band III seems to be determined rather by the point of origin of the tubular portion of the upper median vein than by the tip of vein 12, as this vein often extends considerably beyond the origin of the upper median vein without causing a corresponding broadening distally of the second band. It sometimes happens that vein 12 is unusually short and then the white fascia lies over its tip and over the origin of the upper median vein. On the costa, the inner border of Band III lies just beyond the origin of the upper median, and on the dorsum, the outer border extends almost to the tip of vein 1h. Band IV crosses beyond the tip of vein 1h, and lies over the bases of veins 11 and 2, its outer border being just within the tips of veins 11 and 2. Band V on the costa is placed between veins 11 and 9, on the termen between veins 2 and 6 and lies over the transverse vein. Band VI is placed between veins 9 and 7 on the costa and beyond vein 6 on the termen. Where, as is the case in the immediate ancestral genus, three veins are given off to the termen, the white fascia separating Bands VI and VII lies over the tip of the third of these on the termen, and

over vein 7 on the costa. Band VII crosses the apex of the wing. Thus it will be seen that the position of the bands is largely determined by the position of the longitudinal nervures, the tips of the veins marking the extremities of the unpigmented fasciae separating the bands. In no case in the adult, has this pattern been preserved in its original primitive condition as seven distinct transverse bands; fusions either partial or entire have taken place between two or more adjacent bands. Displacements have also occurred, due to a shrinking away of color from one side of a white interspace and its extension over the white on the other side. Finally, some of the bands may have shrunk away almost entirely.

The following is a list of the species in which the development of the pattern has been traced from the first appearance of color to the adult markings:

Lithocolletis tiliacella Cham.

" *tritaenianella* Cham.

} species in which two or more of the bands have been preserved almost in their primitive condition as respects position and shape.

Lithocolletis crataegella Clem.	species in which changes
" ostryaefoliella Clem.	in shape or position or
" lucidicostella Clem.	both and more or less com-
" morrisella Fitch	plete fusions of some of
" hamadryadella Clem.	the bands have taken place,
" bethunella Cham.	and certain differentia-
" ulmella Cham.	tions and specializations
" aesculisella Cham.	have appeared, such as the
Cremastobombycia ignota F. and B.	development of black scales
	at places other than those
	directly contiguous to the
	white interspaces between
	the bands.

In the following species, the development of the pattern was observed only in part for the purpose of comparing the development of certain characters in these species with that of similar characters in related species, or with a view of determining the relative time of appearance of certain unit characters:

- Lithocolletis hageni F. and B.
- " robiniella Clem.
- " caryaefoliella Clem.
- Cremastobombycia solidaginis F. and B.

In all of the species studied, the wings are at first transparent and glassy in appearance, corresponding to the

period, as observed by Mayer ('96), before the protoplasm has been retracted from the scales. Following this, is the so-called white stage, in which the wings appear by reflected light almost pure white, and by transmitted light pale buffish, due to the haemolymph contained within them. The scales are at this period, colorless and transparent, containing only air. The white stage lasts from one to two days, giving way to a pale yellow over certain defined areas, as the haemolymph enters the scales and the pigment begins to form. This yellow color may be preserved throughout pupal development almost as originally laid down, or it may go through a process of transformation before reaching the adult condition. In either event, it gradually deepens in tint and constitutes the ground color upon which the dark streaks (margins) and spots are to appear. The development of the pattern takes place very rapidly during the last part of the pupal state. The time intervening between the first appearance of a tinge of yellow on the wings and the emergence of the imago is largely dependent upon temperature, and is often less than twenty-four hours. Development takes place more rapidly in day time than at night, and is strikingly retarded during cloudy weather.

Lithocolletis tiliacella Cham.

In the first specimen examined, the wings were removed from the pupa at a very early stage of development. The yellow color is scarcely differentiated from the clear buffish white wing (Fig. 2). The only bands which can be distinguished are II, III and IV. Band II crosses the wing just before the tip of vein 12, thus occupying its primitive and typical position. It is the palest and least defined of any of the three bands present. Its outer edge is definitely defined, but its inner edge fades into the clear basal part of the wing, the color being extended farthest toward the base just within the costal and dorsal margins. Band III has also preserved its primitive position and form. It is somewhat darker than II, but uniformly colored throughout its breadth, the outer edge not darkened. Its width is scarcely greater than that of the clear band preceding it. Band IV is the most deeply colored as well as the broadest of the three bands; it is of the same breadth as in the adult. Even at this early stage it is prolonged outwardly almost to the end of the cell. The entire apical part of the wing and cilia are of the clear whitish color, there being no indication whatever of bands.

The wing in the next stage examined shows considerable advance over the stage just described (Fig. 3). There has

been a decided deepening of color and the adult pattern has been laid down with the possible exception of Bands VI and VII, which have not as yet been clearly differentiated as bands although there is a faint yellow tinge in a few of the scales in the apical portion of the wing. These bands are usually indistinct and sometimes absent even in the adult. Band I is united with Band II along the costa; this condition was apparently not produced by the independent origin of Band I and its later fusion with II, but by a uniform and gradual deepening of the wing below the costa. The outer edge of Band II is now somewhat bent outward in the middle, and the scales in the middle of the outer edge are beginning to deepen in color, thus foreshadowing the appearance of the dark margin, but there is as yet no brown pigment in the scales. Band III is also somewhat bent outwardly as in the adult and its dark margin is present on the costa and dorsum only, the costal margin being much less distinct than the dorsal; neither extends more than a short distance onto the wing proper. The middle of Band IV is faintly connected with a pale band beyond, which represents Band V. Its margins have reached more nearly their adult condition than any other of the wing markings. The margin on the dorsal half is almost as greatly developed as in the adult; that on the costal half is represented only by a few black scales.

The next stage studied shows no further change in the shape or extent of any of the bands, the changes which have taken place being confined to a continuation of processes already begun, namely, the deepening of the outer edge of Band II thus forming the internal margin of the first white fasciae in the adult, the approximation of the costal and dorsal parts of the margin of Band III, so that they are now but little separated, and their darkening to the adult color, the advance of the margins of Band IV to their adult condition, the deepening of Band V so that it now appears quite distinct and as in the adult.

This is the only species studied which shows any distinction between the bands in regard to their relative time of appearance. Bands II, III and IV are the first to appear, and in the youngest specimen examined Band IV was decidedly in advance of the other two as shown by its deeper color and by its extension outwardly in the middle. It is therefore probably safe to assume, that Band IV is in this species, the earliest to appear ontogenetically. As will be shown later, *L. tiliacella* has probably in many respects conserved more closely than any other of the now existing species, the primitive type of color pattern, and hence the sequence observed in the appearance of the bands in the ontogeny may also be true for the phylogeny.

Lithocolletis tritaenianella Cham.

At the earliest stage at which it is possible to discern any indication of marking, five very pale yellow bands are visible upon the wing (Fig. 4). These are uniformly colored and straight and are placed transversely upon the wing, showing no signs of fusion with one another. The first of these is in fact I+II, as shown by the faintly paler streak extending into it from the base of the dorsum. The second, Band III, occupies its usual position, but in this case the position of the white fascia separating it from II is wholly determined by the point of origin of the upper median vein, as vein 12 extends for a considerable distance into Band III. The third, Band IV, is normal in position and shape. That the fourth band is in reality composed of Bands V and VI is shown by its origin just beyond the tips of veins 11 and 2 and by its extension distally over the tips of 9 and 6 which in the primitive color pattern mark the position of the white fascia separating Bands V and VI. Band VII crosses the apex of the wing. The white interspaces between Bands II and III, and between III and IV are of about the same width as in the adult, but that between IV and V VI is considerably wider and shows no indication of the angulation which is present in the adult, that is, Band IV has not yet begun to extend outwardly through the cell. The space separating V+VI from VII is at this

stage about

stage about one-half the width of V+VI and extends entirely across the wing, thus differing strikingly from the condition found in the adult.

The development for some time consists merely in a uniform darkening of the ground color as first laid down without any change in the extent of the bands. At a somewhat later stage, simultaneously with the darkening of the ground color into the adult shade, changes in shape and more complete fusions of some of the bands occur. As soon as the adult color has been attained, the dark margins begin to develop. A specimen examined at this period shows that while no change has taken place in the form or extent of Bands I+II, and III, Band IV has become outwardly angulated as in the adult, thus narrowing, especially in the middle of the wing, the white fascia separating it from V+VI. On the dorsal margin, Bands V, VI and VII are completely fused, the small white costal streak before the apex alone remaining to mark the position of the white fascia between V+VI and VII. The scales along the outer edges of Bands II and III are beginning to show faintly brownish tips, this color being about evenly distributed along the entire edge of Band II; in Band III the color extends farther toward the bases of the scales in the middle of the wing. The scales of the dorsal half of the outer edge of Band IV are dark reddish brown, almost as in the adult, but on the costal half of the wing there is only a very slight

deepening of the yellow color, the margin here being considerably paler than the margins of Bands II and III. There is a very slight deepening of scales on the outer border of Band V+VI. adjacent to the white streak before the apex. The dusting in the apex is dense, the color being darker and more blackish than the outer margin of Band IV, and extends from the white streak well around the apex and along the dorsal margin almost to vein 6. This dusting is considerably greater in extent even in this stage than that of the overwintering forms in any stage.

Lithocolletis crataegella Clem.

This species belongs to that large group in which the imago is characterized by the presence of pairs of opposite white costal and dorsal streaks, that is, all of the original primitive bands have fused at least along the middle of the wing. *L. crataegella* possesses in addition a margined basal streak, external as well as internal margins to the white streaks (i. e., the dark scales developed on both sides of the primitive bands and not only on the outer side, as in the two preceding species), a streak of dark scales along the middle of the wing, a patch of black scales in the apex and the blue iridescence of the scales in the cilia. The study of the development of the wings in this form, should therefore throw light upon the origin and mode of development of the above

characters and indicate their relative time of appearance.

In the earliest stage examined (Fig. 5), at a period when the markings are pale yellowish and but little differentiated from the colorless wing, the pattern strikingly resembles that of the adult insect. The white basal streak is distinctly outlined, beginning at the base of the dorsum, where it seems to be homologous with the white streak separating Bands I and II, beyond this lying over a trachea which extends through the cell just above the middle; Its tip seems to coincide with some portion of the white fascia separating Bands II and III. The white patch near the base of the dorsum is identical with that in the adult, and with the apex of the basal streak seems to constitute the last vestige of the white fascia separating Bands II and III. On the dorsal margin, the outer edge of Band III has shrunk away toward the base, and at the same time there has been a compensating extension of Band IV toward the base, resulting in a displacement of the white streak, so that instead of being over vein 1b, it is basal to it and vein 1b reaches the margin well within Band IV. The first pair of streaks are already separated by a narrow line, which is not nearly as broad internally as in the imago. At this stage the costal white streak is not much narrower on the margin than the dorsal. Bands V, VI and VII are situated normally, except that V on the dorsum extends a little basally

over the tip of vein 2. These bands while quite distinct on the margins and in the cilia, seem to fade away in the middle of the wing. The entire middle of the wing from the tip of the first dorsal white streak almost to the extreme tip of the wing, remains colorless, so that it is not possible to distinguish the bands from the interspaces separating them. A comparison with the adult shows that this area coincides with that to be occupied by the dark streak of scales through the middle and by the apical patch of black scales.

In a specimen somewhat more advanced, there has been a slight deepening of color, but by no means, even in the golden color, has the adult shade been attained. The color is still yellow, with no tinge of brown, unless the slight darkening of the dorsal side of Band IV, especially toward the second white streak, may be regarded as a foreshadowing of that color. The middle of the wing from the tip of the first dorsal streak almost to the apex (except for the grayish black scales to be noted below) still retains its whitish appearance. Just before the apex and beginning just under the tip of vein 7, and extending for a short distance along the underside of 7, are a number of grayish black scales. These appeared first beneath the tip of 7, and were gradually extended toward the base. The patch is broadest toward the apex, where it reaches almost across the wing. The inner edges of the first pair of streaks are more curved than in the preced-

ing specimen as a result of the broadening internally of the yellow line separating them. The scales attached around the apex are yellow and extend in an unbroken line to the second dorsal streak, that is, Bands V, VI and VII have united along the termen. However, the scales whose apices project beyond these and which are destined to constitute the iridescent blue line in the cilia still remain pure white.

A specimen at a somewhat later stage (Fig. 6) shows a little more of the orange brown tint, but the color is nowhere as deep as in the adult. The former colorless area in the middle of the wing is still distinctly set apart from the rest of the wing, but has become narrower, and is beginning to acquire a faintly yellowish tinge. The white streaks are now definitely blocked out due to the curving in of the yellow color; they are however still connected with the whitish middle portion of the wing. The patch of blackish scales near the apex has increased in extent and depth of color until its identity with the patch of black scales in the apex of the adult wing is clearly established. It has now reached its adult condition and no further change takes place. The early origin and differentiation of this patch of scales shows clearly that it is a character quite separate and distinct from the dark line of scales in the adult extending from it toward the base of the wing. The scales around the apex,

yellow in the earlier stages, are now tipped with pale brown, but the outermost row of scales are still whitish as before. There is some deepening of the ground color just before the first and second pairs of streaks, the second dorsal streak however, is the only streak which can be said to have acquired a definite margin and even this is pale brownish. The basal streak remains entirely unmarginated.

In a specimen at a little later stage than that just described internal margins though very pale have appeared along all of the white streaks; that of the second dorsal still continues to be in advance of the others. The margin of the first costal streak has deepened somewhat, and there is a faint suggestion of gray around its tip. A similar pale gray shade extends from the tip of the first dorsal streak through the middle of the wing and around the tip of the second dorsal streak. The ground color along the upper edge of the basal streak is somewhat darkened, but there is no margin.

In a wing at a considerably later period of development, the ground color approaches the adult color over those areas where there are no brown scales. The internal margins of the costal and dorsal streaks as well as the upper margin of the basal streak are dark brown; the external margins of these streaks and the margin around the tip of the basal streak while present are not as dark as in the adult and show

and show a decidedly grayish tinge. This same gray color is prolonged from the tip of the first dorsal streak along the middle of the wing in the area formerly colorless, but is much paler than in the adult. This difference from the adult color is especially noticeable above the patch of black scales, where in the imago there is a decided deepening of color, almost blending with the black patch. There is but very little deepening of color between the first and second dorsal streaks and the margin of the second dorsal streak is neither as deep nor as wide as in the adult. The darkening of scales in the cilia started in earlier stages still continues. There is however no change from the colorless condition of the scales which are to be deep iridescent blue.

The adult coloration appears to be attained several hours previous to emergence. At this time the markings are plainly visible through the pupal envelope. The bluish iridescence in the cilia is now well developed. Obviously this is one of the last characters to appear ontogenetically.

Lithocolletis ostryaefoliella Clem.

This species possesses an apical dot in its typical condition, composed of small black or blackish brown scales arranged in an almost circular shape over the tip of the wing.

In the youngest specimen examined, the wings were

dissected out at a period when they were losing their whitish appearance and becoming faintly banded. The last four bands are straight and placed transversely on the wing, leaving colorless bands between them. The basal portion of the wing is exceedingly pale and the ground color is scarcely discernible on the otherwise colorless wing. The configuration of the color areas is much the same as in the adult, there being the same outward angulation of Band III, internal to the first pair of white streaks. A stripe along the middle of the wing and a white spot on the dorsal margin remain colorless and mark the position of the basal streak and the white dorsal spot in the adult.

At a slightly later stage, the markings just referred to have become a little more distinct; the color is still a very pale straw (Fig. 7). The extreme base of the wing while very pale, is still sufficiently contrasted with the unpigmented areas, to show the outline of the basal streak defined for its whole length. On the dorsal edge, a pale shade broadest on the dorsal margin reaches two-thirds of the way across to the basal streak. On the basal side of this spot the ground color seems a little deeper. Band III, although much angulated outwardly, is not yet connected in the middle of the wing with Band IV; thus the first pair of white streaks are still connected and form an angulated fascia, broadest at its extremities. Bands IV, V, VI and VII re-

main entirely separate, and retain their primitive straight edges with the exception of the inner edge of Band IV which has been somewhat produced toward the base at its extremities. Band III and Band VII are possibly a shade darker than the other portions of the wing, the scales attached around the apex projecting into the cilia are however paler and concolorous with Bands IV, V and VI.

The ground color continues to darken reaching its adult condition at a relatively earlier stage than is the case in *L. crataegella*. At the same time (Fig. 8), the pale yellow spreads onto places originally unpigmented; thus the bands become connected by a paler yellow shade, so that the white fasciae are transformed into pairs of opposite narrow white streaks. At this stage in the development, there are four dorsal as well as four costal streaks. The apical dot is present, dark brown and almost as large as in the imago and very definitely outlined. Around the extreme apex, the scales projecting into the cilia are tipped with brown, this color being deepest just opposite the apical dot, but quickly fading out on either side, so that it does not reach to the last pair of white streaks. The apical spot and these few scales around the apex are the only scales on the wing which show the slightest sign of brown; The bands are however a little deeper yellow on their outer than on their inner borders.

Very soon after the stage just described, the dark margin of the second dorsal streak begins to develop; at this time it consists of a few darker and slightly grayish tinted scales somewhat removed from the dorsal margin. The apical spot is brownish black and seems to have reached its final development. The line in the cilia though darkest immediately opposite the apical spot, is plainly visible from the fourth costal to the third dorsal streak thus passing below the fourth dorsal streak which at this stage has almost disappeared owing to the fusion of Bands.VI and VII.

Very little change is now needed to reach the adult condition. The margins of the second pair of white streaks continue somewhat in advance of the others, and reach their final stage of development a little earlier. All trace of a fourth dorsal streak finally disappears.

Lithocolletis lucidicostella Clem.

At the time of the first appearance of a pale yellow tinge upon the wings, it is possible to discern faintly four bands in the apical half of the wing. Just before the apex within the area occupied by Band VII is a small colorless spot. With the exception of the fact that these four bands are not connected along the middle of the wing, the adult color areas are now laid down. The dorsal portion of Band IV, the most

proximal of these four bands, is continued toward the base as in the adult, by a pale yellow streak along the fold. Its costal portion is preceded by a white streak bordered internally by pale yellow which is extended along the upper median vein to the base.

The apical dot is the first dark mark to make its appearance. While the yellow is still very pale, the scales of the formerly colorless spot near the apex begin to take on a grayish tinge. The deepening of scales over this area seems to take place in very much the same manner as that of the dark scales before the apex in *L. crataegella*.

The apical spot continues to deepen and increase in extent, reaching its adult condition before there is any indication of the formation of dark margins. The development of the apical spot is accompanied by a gradual and uniform deepening of the ground color together with the fusion of all the bands in the middle of the wing, and of VI and VII on the termen. The middle portions of the wing between the apices of the white spots are somewhat paler, showing where the pigment has recently appeared.

The darkening of scales in the cilia around the apex and just below it on the termen, and the dark margins of the first costal and dorsal streaks are the next characters to appear. A wing examined at this stage shows the scales in

the cilia brownish with scarcely a tinge of gray, the margin of the first dorsal streak somewhat paler and brownish yellow, extending from the cilia to vein 2, and the margin of the first costal streak pale and scarcely distinct. These observations are in agreement with those made on *L. crataegella* and *ostreaefoliella*, namely, that the dark markings appear earliest in the apex of the wing on Band VII, and soon after on Band IV.

The process of development consists now merely of the gradual appearance and darkening of the margins of the other streaks and the extension of the line in the cilia to the first dorsal streak.

Lithocolletis morrisella Fitch.

At a period when the entire wing, viewed by transmitted light, seems uniformly colorless, the white markings as seen by reflected light are definitely laid down as they will appear in the adult, and have already acquired the lustrous pearly tint characteristic of the adult. This white appearance is due entirely to a structural modification of the scales, and can not be in any way ascribed to a precocious development of the scales over these areas, since when examined, all of the scales of the wing are seen to be fully developed.

With the first appearance of pigmentation, apale yellow suffuses those portions of the wing only which are destined to be yellow in the adult (Fig. 9). In the basal half of the wing, therefore, the yellow is confined mainly to the region above the fold; there is however a faint yellow tinge just before the dorsal arm of the fascia. There is a scarcely discernible tinge of gray at the base of the dorsum below the basal streak and before the first dorsal streak. At the tip of the wing, over the area to be occupied by the apical dot, the scales are beginning to turn gray, those outermost being the deepest. Otherwise, the areas occupied by gray and black in the adult and by the white streaks, appear by transmitted light uniform and colorless. Examination by reflected light shows that these two kinds of areas are not homologous, since the white streaks stand out clearly as structural modifications, while the scales margining them and those below the fold are duller and lack the pearly luster. The bands and the white fascia and streaks occupy their normal positions. The absence of a white streak over the tip of Vein 7 is accounted for when it is seen that the apical spot has acquired such proportions as to cover the tip of vein 7, which in this and related species reaches the margin nearer to the apex than usual.

In the next stage examined (Fig. 10), the ground color has deepened somewhat, and decidedly more of the grayish tint

has developed. The dorsal part of the wing below the fold, to be occupied by black scales in the adult, is pale gray; beyond the fascia where the scales are merely brown tipped, the color is still yellow, concolorous with the rest of the wing. Internal and external margins of the streaks are beginning to form simultaneously, those of the first costal streak are the deepest. The change is direct from the colorless scales margining the white streaks to pale gray. The black streak in the fold beyond the fascia is at this stage composed of pale gray scales. The apical dot is still pale gray, but the outermost row of scales is much darker and continuous on either side with a line of gray scales extending from the fourth costal streak to the third dorsal streak. The scales whose tips are to form the dark line in the cilia are still white.

On the next wing examined, the gray has decidedly deepened along the dorsal margin, but the golden color has not reached its final condition. The development of the margins has progressed considerably, but now the internal are decidedly in advance of the external margins. The former have a blackish color especially toward the costal margin; the latter are still grayish. The external margin of the first costal streak is deeper than that of the others. The black streak in the fold has increased in size and color until its extent is now definitely defined. The scales around

its outer edge, which in the preceding stage were the only dark ones, are now black. The line in the cilia is gray, but there is no indication of the bluish iridescence.

From this time on, no new characters appear, the development consisting only of a deepening of the colors to their adult condition.

The sequence of colors and the relative time of appearance of the various adult characters is very much the same in *L. robiniella* as in the species just studied. The apical spot and the black streak in the fold reach their final condition at a somewhat earlier stage in comparison with the development of the other markings.

Lithocolletis hageni F. and B.

This species possesses a well-defined apical dot, very decided external margins to the white streaks as well as the usual internal ones, and a dark margin along the upper side of the basal streak. The margin along the upper side of the white basal patch is regarded as homologous with the margin of a basal streak, that along its outer side with the external margin of the white streak primitively separating Bands II and III. The streak of ground color beyond the basal white patch is therefore the dorsal portion of Band III.

Very few specimens of this species were available for

study, but the observations confirm in general those made upon the five preceding species.

The apical dot appears well-defined and blackish at a period when Bands V, VI and VII are still separated from one another by curved white fasciae extending entirely across the wing and into the cilia (Fig. 11). The second pair of white streaks are still connected, but Band IV is beginning to project into them in the middle of the wing. At this time the ground color of the wing is a pale straw and lacks altogether the golden brown of the adult. The internal margins of the first and second streaks are beginning to form. The inner edges of the bands, bordering the streaks outwardly, present much the same appearance as they do in species where the white streaks never acquire external margins, that is, the ground color fades gradually into the white.

A dark line in the cilia begins to form soon after this; the scales showing the brown pigment at this time are not those which will be bluish iridescent in the imago; these latter remain pure white and only acquire their pigment later.

In the third specimen studied, the extent of the white streaks has been finally limited, and the golden brown color of the adult has been attained. All of the internal margins of the streaks, the dark scales at the apex of the first dorsal streak, ~~those connecting the tips of the second pair of~~

streaks and the two leaden colored lines of scales running across the wing from the tips of the third and fourth costal streaks are present. In addition external margins are present on the white basal patch and on the first dorsal streak. All of these borders are as they will appear in the adult. In this specimen there was no indication of a deepening along the upper side of the basal patch. However this observation can not be accepted as altogether reliable in indicating the time of appearance of the margin of the basal streak since the specimen was evidently abnormal, the apical dot not being present. No other specimens were available to decide the point.

Lithocolletis aesculisella Cham.

The species heretofore studied have been those belonging to the group having cylindrical larvae, and characterized by the principal margins of the white streaks being internal. This species and those following have the so-called flat type of larva, and the white streaks of the imagoes have their darkest margins on the outer side. That is, in the former group, the tendency is for the color bands to acquire first, dark margins on their outer edges; in the latter group the condition is reversed and the dark color appears first on the inner edges of the bands.

In *L. aesculisella* at a period when there is scarcely any differentiation between ground color and bands, the pattern appears to be laid down almost as in the adult (Fig. 12). The bands are very pale buff, and judging from their uniform color, appeared simultaneously. The pale shade at the base which separates Bands I and II extends entirely across the wing, but the early fusion of these bands on the costa is foreshadowed by the very faint tinge of buff just making its appearance in the costal portion of the pale fascia. On the extreme costa Band V is indistinctly separated from VI. Band VI is separated from VII by a white streak extending entirely across the wing. With these exceptions, the yellow marks are defined as in the adult. The white oblique dorsal streak extends just within the termen, being separated from the white streak before the apex as in the adult. The distal end of the oblique dorsal streak is probably homologous with the middle portion of the white fascia which in primitive types separates Bands V and VI. In the imago it sometimes exists as a separate small white spot before the apical dusting, and more proximal than the oblique costal streak. Along the termen the cilia are of an unbroken yellow color, showing that at the extreme margin, there has been a complete fusion of Bands V, VI and VII.

Before any of the dark margins begin to appear, the ground color deepens into the orange yellow of the adult.

The external margin of the second fascia, and the dark dusting at the extreme apex are considerably in advance of the other dark markings. The margin of the second fascia, formed by a dark line of scales along the inner border of Band IV, is most distinct in the middle portion of the wing and has not appeared on the extreme dorsal end nor on the costal end beyond the angle. Its color at this stage is brownish. In one specimen, the apical scales are not as dark as the margin of the second fascia; in another of the same age, as indicated by the state of development of the margins, the dusting of the apex is somewhat darker than the margin of this fascia; in both however, the brownish tint is confined to the extreme apex. There is a slight darkening of the scales in the middle of the wing on the inner border of Band III adjacent to the first white fascia, and along the outer side of the oblique dorsal streak.

The dark margins of the fasciae and of the oblique dorsal streak continue to develop, but before they reach their adult condition, the scales on the outer side of the costal spot over vein 11 begin to darken. At this time, the apical dusting is still confined to the apex of the wing and is not extended along the termen toward the tornus. This extension of the dusting toward the tornus is a characteristic of specimens appearing in the summer and does not occur in forms

from overwintering chrysalids. It develops after the other adult characters have appeared.

Lithocolletis bethunella Cham.

In the youngest specimen examined, the ground color is a uniformly pale ochereous, and upon it the extent of the adult markings is quite definitely blocked out (Fig. 13). The white fascia (or second pair of streaks) is however prolonged outwardly at its angle along the wing to a position between the third pair of streaks. A comparison with the adult shows the prolongation of the fascia is occupied by dusting on a whitish ground, that is, these white scales are destined to become black tipped. The third pair of streaks are situated normally over veins 11 and 2 respectively. There is no white spot over the tip of vein 9 on the costa; Bands V and VI have fused. A quadrate area in the apex remains colorless; the portion directly over vein 7 corresponds to the white streak normally situated here, the remainder will be occupied by dark dusting in the adult. The scales around the margin at the apex are yellow; these in the adult will be brown tipped yellow scales.

In a wing at a somewhat later stage, there has been some deepening of the ground color. There is a small patch of scales just beyond vein 7 which are brown tipped and darker

than any other scales on the wing. In the extreme apex, the scales extending over the cilia are not noticeably dark tipped. Dorsal to the dark patch of scales, the scales over the formerly colorless area become gradually paler, until near vein 6, their tips show just a faint tinge of gray. All the scales in the prolonged portion of the fascia are becoming pale gray tipped. There is also a faint gray tinge to the scales just below the tip of the dorsal arm of the fascia, continuous with the gray in the prolonged portion of the fascia. All of these scales are much paler than those in the apex just beyond vein 7, but approach in color those near vein 6.

The margins of the remaining streaks soon make their appearance; the dusting of the apex reaches the adult condition earliest.

A contrast in the sequence of development of dark marks is afforded by *L. caryaefoliella* Clem. In this species the margins of the first and second fasciae develop contemporaneously with a small patch of dusting at the extreme apex; and the margin of the second fascia is entirely complete though not as dark as in the adult, at a stage when there is no indication of dark dusting beyond its angle. This dusting is very variable even in the adult sometimes being very slight. The significance in the difference in development will be discussed later.

Lithocolletis ulmella Cham.

In this species the pale yellow appears simultaneously over all those areas which are to remain yellow in the adult or in which the scales are yellow with brown or blackish tips. The white streaks and the white dusted portions of the wing remain colorless. Thus, the second costal streak is produced for a short distance along the cell, and the wing from vein 7 to the apex is colorless, but the scales around the apex and below the oblique dorsal streak which are yellow with brown tips in the adult have already acquired the pale yellow color.

In the next stage studied, the color has become almost as deep as in the adult. A number of the scales projecting from the extreme tip of the wing over the cilia are brown tipped; these are continued in a broken line through the cilia to the tornus. Over the wing membrane near the apex, in the area which was transparent in the earlier specimen, the scales are becoming dark tipped. These scales are deepest toward the apex of the wing, becoming very pale gray toward the tornus external to the oblique dorsal streak. A few scales along the costa corresponding in position with the dark scales in the adult are beginning to show darker tips. The scales margining the first and second costal streaks, which were whitish before, are now faintly gray. The color is uniformly developed over the whole margin and on the pro-

longed portion of the second streak.

In a specimen a little further advanced than the one just described, the apical dusting is almost as in the adult. This darker color does not quite reach the tornus, that is, the external edge of the white dorsal streak is still margined by pale gray scales as before. The margins of the first and second costal streaks have scarcely changed in color, but the scales in the prolonged portion of the second streak have darkened more rapidly; they are decidedly gray, but much paler than those in the apex. The only new character which has appeared is the dark line through the cilia.

Lithocolletis hamadryadella Clem.

In the earliest stage examined (Fig. 14), the basal third of the wing is almost colorless. At the extreme base on the costal margin is a small patch of pale yellow scales and a little beyond it another similar patch. These two patches of scales form Band I. Beyond these is a somewhat larger patch of pale yellow scales. This is the inner portion of Band II; the line of scales which marks its original outer limit in the adult has not yet acquired any pigment. Band III at this stage is represented by a rather narrow angulated band which extends across the wing some distance before the tip of vein 1b. The white projects into its angle

on the inner side. Band IV is composed of two separate patches of yellow scales, one on the costa and the other on the dorsum. Their pointed apices lie over the bases of veins 11 and 2 respectively, the normal position for Band IV, but on the margins they curve back toward the base so that they are much farther removed from the tips of the veins than usual. The middle of the wing to the apex is colorless. Band V+VI is represented by a patch of scales on either margin. The dorsal patch originates just beyond vein 2 and extends over vein 6; the costal patch originates on the cell about midway between veins 11 and 9 but extends obliquely outward so that the inner edge on the costa is just basal to vein 9 and the outer edge just before vein 7. The white streak over the tip of vein 7 is very narrow and its corresponding dorsal streak is indistinct. The cilia belonging to Band VII are all yellow with a few white scales here and there extending into them. Bands VII, V+VI and IV are some what deeper than Band III; Bands I and II are very pale, their paleness being caused by the large admixture of colorless scales at this stage.

In the next specimen examined, apart from a slight deepening of Band III and those beyond it, the only changes observed are the following. The two basal patches on the costa, belonging to Band I, show a slight admixture of brownish tipped white scales. The third patch (Band II) is now faintly continued to the dorsum by a line of scattered yellow

scales, and just beyond it, in the position normally occupied by the outer margin of Band II, is an angulated line of very faintly yellow scales. This marks the original outer limit (phylogenetically) of Band II. Just before the tip of vein 1b is a similar line of scales running parallel to the dorsal arm of Band III and marking its outer limit. These two lines of scales sometimes do not appear until a much later period in the development. Their time of appearance is largely determined by the number of yellow scales mingled with the dark scales in the adult, since it is only in the yellow scales that the pigment appears early.

In the next stage studied (Fig. 15), Bands I and II in the basal part of the wing remain practically unchanged. Band III is the same in extent, but its color has deepened. Its internal margin is beginning to form, the scales adjacent to the yellow becoming gray tipped. The gray pigment appears directly in the whitish uncolored scales of the previous stage without passing through any of the intermediate steps. In general, the margin is broadest on the costa, becoming narrower and paler below it, and not easily distinguishable toward the dorsum. On its inner edge, the margin is straight or slightly curved as in the imago; on its outer side, the scales project into the angle of the band and fill up the formerly colorless space. The tips of these scales are darker than those of

the margin elsewhere. In this specimen there are only a few scattered yellow scales beyond Band III and no indication whatever of the dark line of scales which is to appear later. The internal margin of Band IV is well marked on its dorsal half, consisting of several rows of dark tipped scales as in the imago. It curves between the two yellow patches, extending to their apices, but not beyond them into the colorless fascia. The costal half of the margin consists only of a few pale gray scales and does not quite reach the dorsal half of the margin. Except for a few very faintly grayish scales above the termen on the inner edge of the dorsal part of Band V+VI, there is no indication whatever of any darkening of scales adjacent to Band V VI. Belonging to Band VII, and beginning just behind vein 7, the scales covering the entire apex of the wing are gray tipped. Some of them, especially on the costal margin, project over the yellow scales which are to form the line in the middle of the cilia. The gray tipped scales of the apex, those between the two parts of Band IV and in the angle of Band III are darker than the other scales forming the margins.

In a specimen at a considerably more advanced stage of development, the scales composing the two patches at the base of the costa are entirely gray tipped and are very much the same as they will appear in the adult. The colorless scales mingled with those forming the proximal part of Band II are beginning to be gray tipped; this is especially noticeable

on the quadrate part above the upper median vein; below it there is only a line of a few scattered gray tipped scales reaching to the dorsum. The line of scales beyond, forming the original outer limit to Band II is pale gray tipped throughout, and though broader on the costa, is complete to the dorsum. The broadening of the internal margin of Band III has continued. Its external margin, separated from the yellow band by white, is indicated by a single line of pale gray tipped scales running from the costa to the cell. The internal margin of Band IV has broadened and deepened and has now probably reached its adult condition. It is not possible to determine whether the development is completed in any single specimen, since there is a great deal of variation on the amount of dusting among the different individuals in this species. In this stage, the scales which in the imago are the most distal of those forming the dark external margin of Band IV are tipped with pale gray and connect with the dusting between the costal and dorsal parts of Band IV. Those on the inner side of the margin which will in a great measure fill up the white space between the margin and the yellow parts of the band are still uncolored. There is a very considerable patch of dusting internal to Band V VI on the dorsal margin, and connected with the apical dusting which has been extended proximally between the parts of V+VI. The costal dusting is not nearly as dark and is somewhat scattered. In addition to the extension of

the apical dusting proximally, there has been an increase in the number of dark scales mingled with the cilia. The dark line through the middle of the cilia formed by brown tipped yellow scales is now quite distinct. At this time most of the dark markings are at least definitely defined in position; there is needed to bring them to their final state only a darkening of those scales already gray tipped and in some places the appearance of pigment in other scales adjacent to these.

In a specimen to be described now, most of these characters have appeared (Fig. 16). The patches of dark gray scales at the base of the costa, and the line of scales beyond the third of these patches have increased and darkened decidedly. The line of scales external to Band III has now become dark gray tipped. External to Band IV the dusting has been extended toward the base so that only a small white streak is left between it and the band on the margins. The dusting in the apex has been much increased and extends along the margin especially on the costa, and connects with the internal dusting of Band V, thus almost obliterating the white streak over vein 7.

Cremastobombycia ignota F. and B.

In the youngest specimen examined, one in which the ground color was pale yellow, the extent and position of all the

adult markings is defined (Fig. 17). The paleness is especially marked toward the apex, where it is difficult to distinguish the markings at all. The white fascia is considerably broader than it will appear later. A careful examination shows it to be composed of two parts, an inner fascia which is to form the white fascia of the adult and in which the scales are whiter and are fully formed, and an outer fascia, where the scales are not as large nor as well developed and are somewhat buffish in color. These scales will later form the black scales of the margin. This same thing is true of the other streaks, but is not as noticeable except in the case of the first costal because of their more irregular shape. The band between the pair of streaks at three-fourths of the wing length and the streak enclosing the apex is, as shown by its position, equivalent to Band V+VI. The white streak before the apex is situated over the tips of veins 7 and 6^{*} respectively.

In a later specimen, the ground color has deepened to that of the adult. The scales in the apex and in the cilia remain concolorous with the wing and are not darker at their tips. The dark external margins of the fascia and streaks are appearing simultaneously and all are equally advanced. The scales forming them correspond in position with the colorless scales which formed the outer part of the fascia in the preceding stage. The pigment, which is pale gray without a tinge of yellow or brown, is evenly distributed throughout the entire scale from

note to page 51.

*
An inconsistency between the position of the apical bands in respect to the dorsal veins in this species and that described as typical for the genus will at once be noticed. In this species the white streak separating Bands VI and VII is situated over the tip of vein 6; Band V+VI extends over the tip of vein 5. In other species where V and VI are fused, they cover the tip of vein 6, or where a white streak separates them, it is placed over vein 6, and there is no vein lying between Bands VI and VII. This at once suggests the possibility that the interpretation by systematists of the venation beyond vein 2 is incorrect and that where but one vein reaches the termen, it is vein 5. A more extended study and analysis of the markings of related genera would be necessary to decide the question.

the base to the tip. None of the internal margins has appeared.

In a later stage the external margins are black as in the adult, and internal margins are present on the costal end of the first white streak and the fascia. There are no internal margins on the pair of streaks at three-fourths. As margins of these streaks are not always present in the imago, it is impossible to determine conclusively whether they normally appear after the internal margins of the fascia and the first streak. However as will be shown later in the discussion, variable characters tend to appear later in the ontogeny than the fixed characters of a species.

The observations on the development of color in the wings of *C. solidiginis* agree very closely with those on the preceding species. The configuration of the color areas at their first appearance is the same as that of the adult. In this species however, the scales which are to form the dark margins in the adult are pale yellow, instead of, as in *ignota*, being colorless and not fully formed. A comparison with the adult shows that these are dark tipped yellow scales, the dark pigment being found at the tip of the scales and not, as in *ignota*, almost uniformly distributed throughout the entire scale.

IV. Discussion and Conclusions.

In general, I have found that the action of three processes is sufficient to explain the transformation of the seven primitive bands into the several existing patterns of the ground color. These three processes may be stated thus:

(a) The middle portion of a band may be produced distally until it comes in contact with the band beyond it. (b) The extremities of a band may be broadened by being produced proximally. (c) The extremities of a band may be narrowed by the retraction of pigment from their outer edges. These three processes may act separately or in combination; the particular pattern produced is the resultant of their combined activity. The first two of these laws are based chiefly upon the changes observed during pupal development, the third law is deduced from adult characters, since the changes are such as can not be observed directly. The evidence in detail is as follows:

In *L. tiliacella* (Fig. 18), seven distinct transverse bands of ground color are laid down; of these, those numbered II, III and IV appear first; following these, Band I, at the base of the wing, appears continuous in the costal half of the wing with II; it is however sufficiently separated from it by the difference in time of appearance. The three bands in the apex of the wing appear last and undergo no change; the connection of Band V with IV is brought about entirely by

the extension outwardly of IV along the middle of the wing. The changes in Bands II and III are brought about by the spreading of the color onto areas formerly unpigmented, that is, the fascia between II and III is narrowed by the very slight growth distally of II along the middle of the wing, its extremities remaining fixed; and by the extension proximally of III chiefly along the margins. Band IV reaches its adult configuration earliest; it is also the earliest to acquire the black pigment on its outer edge. This does not appear in the middle of the wing where the band has extended outwardly uniting with V. The outer edges of the extremities of Band III have remained constant in position and the dark scales appear first here. In Band II there has been the least change in shape; the deepening of the pigment along its outer edge occurs more uniformly. From this it follows that while the general tendency is for dark pigment to develop along the outer edges of bands adjacent to unpigmented areas, the precise time of its appearance along any band or portion of a band in relation to other bands or portions of the same band is determined by the time when such bands or portions of bands reach their adult shape and color. The outer edge of a band in direct contact with another band acquires no dark pigment. It would appear from the observations on this species, that the bands in their primitive condition are narrower than they are in the adult. A fascia may be narrowed by the uniform

spreading of a band toward the base.

These conclusions are corroborated by the observations on *L. tritaenianella*; all the bands however appear simultaneously and at this time all are straight. There is however a reduction in the apparent number of bands, V and VI being completely united. Band IV seems no further advanced than the others toward the adult condition; as in *tiliacella*, development must take place more rapidly, since its margins reach their adult condition before those of the other bands. Here also is the first manifestation of that tendency, so characteristic of all the more highly differentiated species of the genus, toward the darkening of scales in the apex. In this species these scales are scattered over the entire apex instead of being limited to a definitely defined area, where the scales are modified structurally. This species does not in any stage, show the primitive type of marking; a considerable amount of development is however necessary before the color areas attain their definitive final extent.

In *L. crataegella*, *ostreaefoliella*, *lucidicostella*, *hageni* and *morrisella*, in the basal half of the wing, where in the adult there is the greatest divergence from a transversely banded type of marking, the color areas, upon the first appearance of a uniform pale yellowish, have almost exactly the same shape and extent as in the adult. They undergo very little change during development, except that in these species

as well as in *tiliacella* and *tritaenianella*, there is a progressive and gradual deepening of the ground color. In the youngest specimens of *ostryaefoliella* observed (Fig. 7) the first pair of streaks are still connected; very soon however they become separated by the union of Band III with IV.

In the apical half of the wing, Bands IV, V and VI appear as straight transverse bands (except in *morrisella*); the transformation of the unpigmented fasciae between them and between IV and V into pairs of opposite streaks is brought about by the outward extension of Bands IV, V and VI along the cell in a manner similar to that previously observed for Band IV in *tiliacella* and *tritaenianella*. The obliteration of a white streak is brought about by the inward extension of the extremity of a band to meet the outer edge of the preceding band. In *morrisella* the pattern is predetermined from the outset; the white fascia and streaks being produced by structurally modified scales, which are destined never to acquire pigment.

There are no reasons favoring the view that such a type of marking as that found in *crataegella* is primitive: there are many reasons for regarding it as having been produced through a long process of evolution. It is a matter of general observation that the pale colors appear first ontogenetically, black of the pigmental colors being last to appear; it has been inferred that the same is true also for the phylog-

eny. In the adults of these species, there have developed, in addition to the usual dark markings adjacent to the unpigmented areas, definitely limited black spots and streaks in the apex. The scales thus pigmented are also differentiated structurally from the surrounding scales by their smaller size. There is no such structural modification of the dark tipped scales in the apex of tritaenianella. Obviously a considerable period of time must have been required for the final differentiation of such characters as these. That these species have undergone an extensive process of differentiation in the production of certain characters of a kind which can only be acquired late in racial development, renders it highly probable that there has also been a far-reaching modification from the ancestral condition of the extent of the color areas. These phylogenetic changes are scarcely or not at all repeated in the ontogeny. Three primitive bands are still preserved during the early stages in the apex of the wing; the band proximal to these shows unmistakable signs of its origin from a straight transverse band, its outer edge being straight. We may therefore with reasonable certainty conclude that the color pattern of the basal part of the wing may be traced back through a series of phyletic changes to its origin from the first three primitive bands.

The ontogeny offers no direct testimony of the means by which these results have been accomplished; it has given

however visible evidence of two actual dynamic methods by which changes have been wrought, namely, the middle portion of each band may be produced distally until it comes in contact with the band beyond it; the extremities of a band may be broadened by being produced proximally. Thus are produced first, angulated fasciae, second, slightly oblique pairs of opposite streaks; the final effect of the second of the above processes if acting alone is the entire obliteration of the white streaks. That a third process has been at work is indicated by observations upon adult forms. The dorsal of the first pair of white streaks in *L. crataegella* does not occupy its primitive position over vein 1b, but has been displaced toward the base and vein 1b reaches the margin within Band IV, that is, there has been an extension of the extremity of Band IV in this direction over the area formerly white. But since a white streak still remains, there must have been a compensating drawing away of the outer edge of Band III at its extremity. Such a withdrawal of pigment can not of course be observed ontogenetically. A third dynamic process in the transformation may therefore be stated thus: the extremities of a band may be narrowed by the retraction of pigment from their outer edges. This is an example of the shrinking away of a band at one end. In this case the shrinking takes place at the outer edge of the band only. The result of the combined action of the second and third of these processes is the pro-

gressive movement of the end of the band toward the base.

These three processes are sufficient to explain the origin of all the types of marking in this genus; the specific results in any case are due to the manner and extent of their action, that is, whether they act singly or together, and to the relative rapidity of action of the three processes.

In the second division of the genus, the extent of the areas of ground color undergoes very little change during development. The ground color appears in the earliest stages over those areas which in the adult are occupied by yellow or reddish yellow scales, or by dark tipped yellow scales. The scales which in the adult are white with dark brown, gray or black tips, do not receive pigment until much later; they then pass directly to gray or brownish gray and thence to black, without passing through the intermediate yellowish and brownish shades. The tendency for dark pigment to develop along the edges of bands adjacent to unpigmented areas is exemplified in this group also, with this difference however, that it appears first along the inner edge of a band. When dark pigment develops in addition along the outer edge it appears at a later period. The converse is true in the first division of the genus; the dark margin appears earlier on the outer side of a band. I can offer no explanation of the original cause of the difference in direction of development; the result in either case seems to be the expression of the same

general tendency in development, acting however with different degrees of intensity on either side of a band." It would seem that the development of unusually dark pigment on one side of a band — the acceleration of chemical processes over a localized area — retards development on the other side.

The ontogeny within this division affords very little evidence of the operation of the first two processes of evolution defined earlier in this discussion. However the shape of the bands, and the separation of the white fasciae into opposite spots, with the total obliteration of some of the spots, is sufficient proof that these forces have acted during the evolution of the species.

L. hamadryadella alone, of those observed, shows the outward prolongation of the middle of a band; the gradual extension distally of the dark dusting between the dorsal and costal portions of Band V+VI and its final contact with the apical dusting (Figs. 15, 16) is an example of the working of this law. The third law postulated to explain the displacement of oblique streaks toward the base receives decisive confirmation from the adult markings of the same species. A narrow line of scales crosses the wing beyond the yellow portions of each of Bands II, III and IV, being separated from them by white. These scales occupy positions corresponding to the outer margins of these bands; ontogenetically the dark pigment develops in them after it has appeared on the inner margins of

these bands. The conclusion is apparent that these lines of scales mark the earlier phylogenetic limits of these bands. The bands have shrunk away, most rapidly on the costa and dorsum, leaving behind them the margins as visible evidences of the process.

In *L. tiliacella* (Fig. 18), which from its conservation of the greatest number of bands in a primitive straight condition, the very pale ground color, and the entire absence of any dark scales in some of the bands, may be regarded as the most primitive of the American species, there is a difference in the time of appearance of the bands. In the more advanced species, the bands appear at the same time. Evidently then in the higher species, there is a hastening and crowding together of the earlier stages, so that the bands which formerly appeared in sequence now appear contemporaneously. Those in the apex of the wing, which have experienced the least modification during the phylogenetic development of the species, alone recapitulate the racial history during their ontogenetic development.

The discussion heretofore has dealt chiefly with the processes which effect the final limitation and configuration of the ground color. The general tendency toward the production of dark pigment in rows of scales adjacent to unpigmented areas has also been noted. These streaks of dark scales, which are usually transverse, and the various other characteristics,

such as the apical spot, the longitudinal streak of black scales in the apex and the black streak in the fold properly constitute the markings, in distinction to the ground color, and are superimposed upon it.. While the progressive change in the configuration of the ground color is the important factor in determining the general evolution of the genus, and the different stages at which development has halted form the starting points for the differentiation of the several groups of species, the development of the markings is the important factor in determining the phylogenetic sequence of the individual species within each group. A knowledge of their mode of origin and relative time of appearance is therefore essential.

In *L. tiliacella* and *tritaenianella*, it was seen that the dark margin develops first along the edge of Band IV, which is the first band to reach its adult shape. In *L. tiliacella*, the outer edge of this band has become fixed before all of the bands have even been laid down. The dark margin appears toward the costa and dorsum, in places where the outer edges of the band have undergone no change whatever since the first appearance of color. The dorsal margin seems to be in advance of the costal. There is no darkening of pigment along the bands in the apex, which appear comparatively late. From these observations it appears that in the ontogeny the dark margin develops earliest along the edge of that band which first reaches its definitive adult condition. Before

dark margins can develop, the edge of a band must have remained fixed for an appreciable period of time.

In *I. crataegella*, *ostreaefoliella* and *lucidicostella*, the dark margin on Band IV is also the first to appear. The apparent contradiction to the principle just laid down that a dark margin develops earliest along the edge of the band that has first reached its definitive adult condition, lies in the fact that in these species the color areas in the basal half of the wing are defined at the outset almost as in the adult, while the bands in the apex repeat the racial development. It might be expected then that the margin would appear earliest along the first pair of streaks. It has however required a much longer time in the evolution of the species for the basal half of the wing to acquire its present aspect; the development in the apical half has come to a standstill comparatively early in the phylogenetic history of the species. The observed recapitulation in the apical three or four bands during the ontogenetic development, of the steps in the racial differentiation of the species, is in harmony with the conclusions of other investigators that it is only among primitive forms that anything approaching a complete repetition of phylogenetic changes is to be found in the ontogeny.

The apex of the wing (in respect to the conservation of primitive color areas) may be regarded as primitive in comparison to the base of the wing. In the phylogenetic

development of this type of marking therefore, it is possible that the margins appeared on Band IV while the basal half of the wing was still under the influence of dynamic forces producing constant changes in the outlines of the areas of ground color. No margins could have appeared in the basal half of the wing until after these outlines had become permanent. Some of these changes, as has been already shown, are such as can not be repeated during pupal development. Hence the color areas in the basal half of the wing tend to be laid down in their final shape, The sequence of the appearance of dark markings, which are in reality a second series of transverse bands superimposed upon an earlier set, follows the same order for the ontogeny as for the phylogeny, that is, in this second and more recent set of characters there is an actual recapitulation. The margins of Bands V and VI appear later, corresponding therefore to the sequence in the time of appearance of these bands phylogenetically, hypothetically based upon that of *L. tiliacella*. The margin of the upper side of the basal streak corresponds in time to the outer margins of the bands; it appears before inner margins develop. An outer margin of a band tends to appear first near the costa or dorsum, an inner margin near the middle of the wing, that is, at the apex of the outer side of a white streak, these being the parts of the edges of the bands which have reached their permanent position earliest. Therefore, the relative

time of appearance of the dark margin of any band in the ontogeny is dependent upon the time when the edge of that band became fixed in the phylogeny.

In *L. morrisella*, margins are formed almost simultaneously on either side of the white streaks, by a direct change to gray and thence to black. The pigment in the other black scales develops in a similar manner without passing through the usual intermediate stages. The gray and black pigments make their first appearance at an early stage, while the ground color is still pale yellow. The structural differentiation of the white scales, the massing of black scales in the dorsal half of the wing, the exceedingly large apical spot and the black longitudinal streak in the fold all indicate the very high phylogenetic position of this species. Upon the addition of these newer characters, the earlier ones were crowded closer together and ^upushed farther back into the ontogeny, resulting in their contemporaneous development.

In the species of the second division of the genus, dark margins develop in conformity with the principles already enunciated. There are certain minor differences between this and the preceding division attendant upon the original unexplained diversity in the inherent tendencies of the two divisions. The dark margin appears first on Band IV in the middle of its inner edge, in contrast to its appearance in the other division on the outer side and near each end of this band;

the same is true for Band III. This is ^anecessary consequence of the action of the three general processes of evolution; the middle of the inner edge of any band remains stationary and hence a margin will develop here earlier than at the extremities of the band.

In *Cremastobombycia ignota*, the development is very similar to that of the species of the "flat-larval group". The margins appear almost simultaneously, the scales changing directly from colorless to gray and thence to black. These scales, at the time the yellow ground color spreads over the wing, are not fully formed, thus contrasting with the similarly unpigmented, but fully developed scales belonging to the white fascia and streaks. In all other species examined the scales were all equally and fully formed at the time of the first appearance of pigment in any part of the wing.

In many species these dark streaks adjacent to white are the only defined dark markings present; there may be a few scattered darker tipped scales in the apex. An increase in the amount of dark pigment producing additional dark markings manifests itself in either of two ways. (1) The number of scales thus affected may be increased, so that the actual extent of the wing occupied by dark tipped scales is greater. This is the direction that evolution has taken in the species of the "flat-larval group", and in a few of the species of the "cylindrical-larval group" (e.g. *celtisella* and *celtifol-*

iella). Often, among the more highly differentiated of the species of the "flat-larval group", the entire apex of the wing is covered with black tipped scales (e.g. agrifoliella). Similar areas may develop in other parts of the wing; thus a patch of dark tipped scales may extend outwards from the angle of a fascia (e.g. bethunella). (2) There may be a concentration of pigment in comparatively few scales, which with increasing differentiation tend to be segregated in definitely limited areas marked out by structural modifications of the scales (e.g. lucidicostella and crataegella). In these case, the scales are pigmented almost to their bases, not merely dark tipped. With the single exception of obstrictella among the species of the second division of the genus, this tendency is confined to the species of the "cylindrical larval group", where it manifests itself in the apex either as an apical dot or as a somewhat elongate or irregular patch of scales, broadest just before the tip of the wing. A similar longitudinal streak of black scales is present in the fold in robiniella, uhlerella and morrisella.

Finally, there may be a decided deepening of the ground color itself between the white streaks. This process has reached its highest development in robiniella, uhlerella and morrisella.

In the ontogeny, the development of all of these specializations has been much abridged, and concomitant with this,

their time of appearance has been pushed back farther and farther into the earlier stages of pupal development. The dark tipped scales remain colorless during the time the yellow scales are attaining their adult condition; later they change directly to gray and black. The pigment in the areas of dark tipped scales in the apex and beyond the fasciae often appears simultaneously with that of the margins. Some variation is to be noticed here; in *L. bethunella* the gray pigment appears in all the scales beyond the fascia, simultaneously with the beginning of the formation of the dark margin; in *L. caryae-foliella* the dark margin of the fascia is complete before any pigment has developed in the area beyond it. In the imago the patch of dusting beyond the fascia is an established constant character in *bethunella*; in *caryae-foliella* the amount of such dusting is very variable, indicating its recent appearance in the species.

It would seem then that only those characters permanently established and of long standing in a species exhibit this precocity of development; recently acquired or variable characters appear ontogenetically in the order of their phylogenetic sequence.

This conclusion is confirmed by observations upon the mode of development ontogenetically of other analogous dark markings. Comparison of imagoes indicates that the apical spot and the black patch in the apex have originated phylogen-

etically earlier than the streak of brown scales along the middle of the wing, but later than the dark internal margins of the white fasciae and streaks. In *L. crataegella* the pigment in the scales of the black patch before the apex, which is unquestionable a characteristic only acquired through differentiation extending over a long period of time, appears earlier than that in the brown scales extending along the middle of the wing, and reaches its definitive adult condition while the latter are still wholly unpigmented. In *L. hageni* also, the apical spot appears sooner than the dark scales in the middle of the wing beyond the tip of the first dorsal streak.

Such specializations as these can not however have originated very early in the evolution of a species; and the observed phenomenon of their unduly precocious appearance and rapid development in the ontogeny requires additional explanation. In *L. crataegella*, *ostreaefoliella*, *lucidicostella*, *hageni* and *morrisella* these were the first dark markings to appear. The first tinge of gray appeared before the ground color itself had reached its adult shade or rarely even before it had reached its adult configuration. It is possible that physiological causes act directly toward this end. In the racial development, the segregation of black scales over a limited area and the later modification of these scales structurally has been accomplished gradually; the results have become permanent in the species, and the scales when first formed

before any pigment has entered them, have a structure identical with that acquired late in phylogenetic development. It is suggested in explanation of the phenomenon of the early appearance of black pigment in them, that the concentration of pigment-forming substances within a smaller space — the interior of these smaller scales — results in a more intense chemical action over a localized area and thus hastens development.

The general conclusions which have been drawn from the study of pupal development may be summarized as follows:

1. The primitive type of color pattern consists of a series of seven transverse bands, which, except the first, cross the wing perpendicular to the costal margin and are not wider than the unpigmented fasciae between them. Their positions are determined by the course of the longitudinal nervures.

2. In the evolution of the genus, changes in extent alone of bands are brought about by the uniform spreading of the pigment toward the base, the edges of the bands remaining straight. Changes in the extent and form of these bands have taken place through the action of any or all of the three following dynamic processes: (a) The middle portion of a band may be produced distally until it comes in contact with the band beyond it. (b) The extremities of a band may be broadened by being produced proximally. (c) The extremities of a band may be narrowed by the retraction of pigment from their

outer edges. The action of the first two may be observed directly, the third is an inference from a comparison of adult markings.

3. The bands, either in their primitive shape or as modified through the course of evolution, constitute the ground color upon which a second darker series of transverse characters is superimposed. These are properly termed the markings, and appear at the limits between ground color and unpigmented areas. Their relative time of appearance ontogenetically is dependent upon the time when that portion of the edge of a band has become fixed in the phylogeny.

4. Later in the phylogenetic history, spots and longitudinal black markings may appear. For reasons not fully understood, certain of these markings appear earliest in the ontogeny.

5. Recapitulation in the ontogeny is at most only partial and is confined to those species or to those parts of the wings in which there has been the least advance from a primitive condition. Here also a distinction must be made between ground color and markings.

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Legend to accompany figures.

- Fig. 1. Hypothetical primitive color pattern of the forewing of *Lithocolletis*.
- Fig. 2. Early stage in the development of color in the wing of *L. tiliacella*.
- Fig. 3. Later stage in the development of color in the wing of *L. tiliacella*.
- Fig. 4. Early stage in the development of color in the wing of *L. tritaenianella* .
- Fig. 5. Early stage in the development of color in the wing of *L. crataegella*.
- Fig. 6. Later stage in the development of color in the wing of *L. crataegella*.
- Fig. 7. Early stage in the development of color in the wing of *L. ostryaefoliella*.
- Fig. 8. Later stage in the development of color in the wing of *L. ostryaefoliella*.
- Fig. 9. Early stage in the development of color in the wing of *L. morrisella*.
- Fig. 10. Later stage in the development of color in the wing of *L. morrisella*.
- Fig. 11. Wing of *L. hageni* at the first appearance of the dark markings.

Legend to accompany figures (continued).

- Fig. 12. Early stage in the development of color in the wing of *L. aesculisolla*.
- Fig. 13. Early stage in the development of color in the wing of *L. bethunella*.
- Fig. 14. Early stage in the development of color in the wing of *L. hamadryadella*.
- Fig. 15. Later stage in the development of color in the wing of *L. hamadryadella*.
- Fig. 16. Wing of *L. hamadryadella* near the end of the pupal state.
- Fig. 17. Early stage in the development of color in the wing of *C. ignota*.
- Fig. 18. Forewing of *L. tiliacella*.

Legend to accompany figures (continued).

- Fig. 12. Early stage in the development of color in the wing of *L. aesculisella*.
- Fig. 13. Early stage in the development of color in the wing of *L. bethunella*.
- Fig. 14. Early stage in the development of color in the wing of *L. hamadryadella*.
- Fig. 15. Later stage in the development of color in the wing of *L. hamadryadella*.
- Fig. 16. Wing of *L. hamadryadella* near the end of the pupal state.
- Fig. 17. Early stage in the development of color in the wing of *C. ignota*.
- Fig. 18. Forewing of *L. tiliacella*.