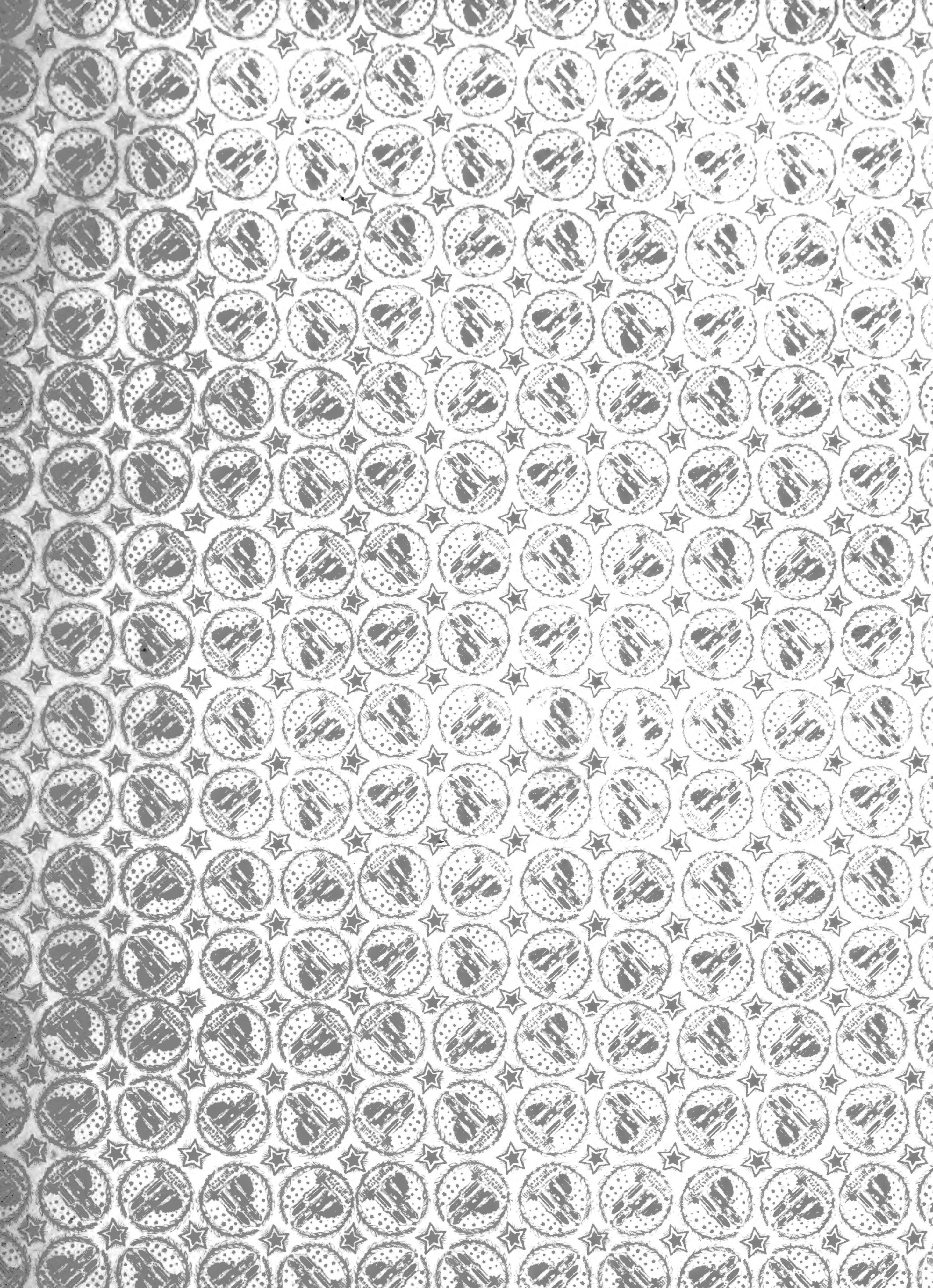
PARTRIDGE

The Tracheation of the Pupal Wings of some Lepidoptera

Entomology

M. S.

1914



THE TRACHEATION OF THE PUPAL WINGS OF SOME LEPIDOPTERA

BY

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B. S. University of Illinois, 1913.

THESIS

Submitted in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

IN ENTOMOLOGY

IN

THE GRADUATE SCHOOL

OF THE

UNIVERSITY OF ILLINOIS

1914

UNIVERSITY OF ILLINOIS

THE GRADUATE SCHOOL

June 1st 1904

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY

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ENTITLED The Tracheation of the Pupal Wings of some Lepidoptera

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE

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on
Final Examination

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I INTRODUCTION

The study of the wings of insects has been one of the most fruitful fields of entomology. The accessibility and the variability of the venation has attracted the attention of practically all students of entomology at one time or another. Here, as in no other organ of insects, there is found opportunity to determine the phylogeny of the different groups. The systematist finds the numberless morphological adaptations of the wing veins invaluable in classification because of the ease with which they can be observed.

Comstock and Needham were among the first to point out the close relation existing between the pupal wing tracheae and the adult wing veins. They made a study of many insects representing all the more important orders, and found that the veins and tracheae were closely related in those orders in which the tracheae precede the veins as ordinarily stated. In certain groups the tracheae do not enter the wing until the veins are fully formed and are, therefore, valueless in the determination of their homology. The Lepidoptera belong to the former class, in which a study of the tracheation aids in determining the homology of the wing veins.

Comstock and Needham also proposed a hypothetical type of the primitive nymphal wing tracheation (Fig. 1) from which, they affirmed, all types of wing venation could be determined. Because their work dealt with all groups of insects, a comprehensive system of nomenclature was devised which could be applied to the wing veins and cells. This is a modification of the system proposed by Redtenbacher; but the premedia and post media of that author are omitted. The nomenclature of Comstock and Needham has been adopted.

Spuler, in his study of the venation of Lepidoptera, also developed a hypothetical type of wing tracheation, but this was applied only to the Lepidoptera. He omitted costa and the fourth branch of media, and showed the third anal vein of the fore wing with two branches. He also figured both fore and hind wings with slight differences.

In 1902, Enderlein published a paper which dealt with the pupal wing tracheation of a few Lepidoptera. He showed the relationship existing between the tracheal system of the body and that of the wing. As he studied only specialized forms, he associated media with the cubito-anal group of tracheae. Media undoubtedly belongs in the radio-medial group, as shown by Comstock and Needham.

Enderlein divided the wing tracheae posterior to cubitus into two groups, the anal tracheae and the axillaries. The axillary tracheae are homologous with the third anal trachea of Comstock and Needham; and the latter name has been retained here. In the Lepidoptera this trachea has two branches in both fore and hind wings in the generalized forms and in the fore wings of specialized forms. If these branches are represented by veins in the adult wing, it is usually only the anterior branch that is preserved.

The pupal wings studied by Enderlein were those of Antheraea pernyi, Sphinx pinastri, Harpyia vinula, and Pieris brassicae. Although the title of the paper is "Eine einseitige Hemmungsbildung bei Telea polyphemus vom ontogenetischen Standpunkt", he did not study the pupal wings of Telea polyphemus.

MacGillivray, 1912, published an account of the venation and tracheation of Stenopis thule. This insect shows a two-branched subcosta and a five-branched radiusin both wings and two ~~a~~anal tracheae

and veins in the fore wing and three in the hind wing. This form approaches the hypothetical type of Comstock and Needham very closely. It has probably the most generalized wing venation of the Lepidoptera.

Considerable light is thrown on the relationship of the pupal wing tracheation and the venation of the adult wing, if the development of a wing of a butterfly or moth be considered. Mercer, '98, made such a study of the development of the wings of Pieris rapae, and the statements made in the following pages concerning the development of wings are based on his discussion of the subject.

The first stage in the development of a wing is a thickening of the cells of the hypodermis, the formation of an imaginal disk on the side of the thoracic segment at the point where the wing is present in the adult. This condition is found in the youngest larva and is probably present in the embryo, though none were examined by him.

When the larva is a few hours old, at most, a slight depression begins at the center of the imaginal disk. A pocket-like structure is formed by this invagination. The process is very slow at first but growth is more rapid as development proceeds. This stage of development is completed about the time of the third moult of the larva, when an evagination commences to grow from the bottom of the pocket. This evagination proceeds rather rapidly, and the evaginated portion, or wing fundament, remains inside the invagination until just before pupation, when it is pushed out through the mouth of the invagination. Its position then is between the hypodermis and the cuticle.

A supply of air must be furnished the wing fundament throughout its growth. This is accomplished in various ways at the different stages of its development. Until the evagination of the wing is com-

menced, the air is supplied by the tracheae of the body. After the evagination has reached any considerable size, this method of air supply becomes inadequate, and a special tracheal system must be developed for each wing.

During the fourth larval stage, tracheoles are developed within the cells of the epithelium of the large lateral longitudinal body trachea. This trachea passes close to the mouth of the evagination and has furnished the air supply up to this period. These tracheoles appear as bundles of coiled capillary air tubes practically filling the mother cells of the tracheal epithelium. There can be no communication with the lumen of the body trachea until the intima lining this trachea is removed at the fourth, the next, moult. The tracheoles then unroll and push out into the wing fundament, following the lymph spaces, which later develop into veins. These tracheoles are known as the primary tracheoles to distinguish them from a different set developed later from the pupal wing trachea.

Shortly before air is admitted into the tracheoles, a number of evaginations are formed from the epithelium of the same trachea that gave rise to the tracheoles. During the fifth larval stage these evaginations grow and push out into the wing fundament, and, in the course of their development, definite branches are formed. These constitute the permanent tracheal system of the pupal wing.

The growing tracheae enter the wing through the lymph spaces, as did the tracheoles. They are not functional until the final larval moult because the intima of the body trachea closes their mouths. The removal of this intima allows the air to enter the wing tracheae.

During the pupal period, the epithelium of the wing tracheae gives rise to a number of tracheoles which are developed from mother

cells in a similar manner to the primary tracheoles. These are known as the secondary tracheoles to distinguish them from the earlier system. They aerate the region of the pupal wing between the main tracheae, the wing membrane.

The veins, that is the cuticular framework of the wing, are formed during the pupal period after the entrance of the wing tracheae. The vein cavities, however, are present from the time the two hypodermal layers of the wing fundament come together during the fourth larval stage. These cavities are the passages through which the primary tracheoles and the tracheae enter the wing fundament. In some cases, however, Mercer found that the formation of a distinct vein cavity follows rather than precedes the entrance of a trachea into a particular part of the wing. This, however, is not the usual method of development.

It would seem that the pupal wing tracheae outline an early stage in the development of the wing veins, because the tracheae enter along the lines of the vein cavities present in the larval wing. This condition is analagous to that of an exposed but undeveloped photographic plate. The developing veins are present, but it is very difficult or impossible to see them, as is the case of the image on the plate. The tracheae enter these cavities and become filled with air, and it is then just as simple a matter to locate the vein cavities as it is to see the image after the plate is developed.

However, it is immaterial in this discussion whether the vein cavities are considered as preceding the tracheae in time of development or vice versa. A relationship, and a very close one, exists between the tracheae and the veins. If the veins are present before the tracheae, the latter outline their position and show an earlier,

and hence more generalized condition in their development. If the tracheae precede the veins, they they show a more generalized condition of the veins because the latter are formed directly about them.

When tracheae are found persisting where no cuticular veins are developed in the adult wing, it may be assumed that specialization by reduction has taken place in that region. It seems evident, therefore, that a study of the tracheation of pupal wings should throw light on the manner in which the veins have been modified. This is the initial object of this paper.

II PREPARATION OF MATERIAL

Owing to the changes that are occurring in the pupal wings of insects, a method that is satisfactory at one period of development may be absolutely worthless at another.

The simplest method followed is that used in the preparation of the youngest pupal wings that were studied. The wings were dissected out of the pupal cases and were washed in clear water. The wings were then floated on the surface of the water to straighten them out and placed upon a microscope slide, where they were allowed to dry. No cover glass was used.

Preparations made in this way are permanent, some of the specimens made two years ago are in as good condition as those made three weeks ago. They are very resistent to bad usage and may be considered about as fragile as photographic negatives. If photographs of such mounts are desired, they should be taken without wetting the specimen. As the tracheae crack somewhat in drying, water is admitted into the tracheae through the openings. The tracheae will not show well in the photograph, as they are filled with the mounting medium.

The above method is not satisfactory in the preparation of those wings in which the veins have begun to thicken. These should be photographed before they are allowed to dry, and may be hardened in 4% formol,as recommended by Comstock and Needham, if desired. If these specimens are allowed to dry, the veins disappear and only the tracheae can be identified.

In the case of those wings in which the scales have begun to appear, the wings need to be cleared before the tracheae can be seen. Glycerin jelly has usually been used for this purpose, but much better results were secured through the use of glycerin. A large percentage of failures occurs when glycerin jelly is used, as the tracheae frequently become filled with the mounting medium, owing to the heat which must be used. There are no failures when glycerin is used; all of the specimens make good mounts. Neither method gives a permanent mount, and if a record of the wing is desired, it must be photographed.

The operation of this method is simple; the wings are dissected, washed in water,and placed on a slide. One or more drops of glycerin are added and a coverglass is placed on the mount. It should stand for half a day or more to allow the object to clear, when it can be photographed. In from three to seven days after the mount is made, the tracheae become filled with glycerin, and the mount is then practically worthless. This method is far superior to mounting in glycerin jelly because such mounts frequently become so clear in a few hours as to be worthless for photography.

III THE TRACHEATION AND VENATION

The venation and tracheation of the fore and hind wings of generalized Lepidoptera, such as Stenopis thule, are very similar in

character. This condition is characteristic of generalized insects of most orders and indicates that the two pairs of wings are homodynamous in origin. All recent investigators have recognized this condition; and Comstock and Needham have proposed a single hypothetical type of primitive wing tracheation (Fig. 1) as characteristic of both the fore and the hind wings.

In the more specialized Lepidoptera, the Frenatae, specialization has occurred in both wings. Owing to the difference in the function of the two pairs of wings, the modifications which have occurred are very different in character. The object,which is attained,is the formation of a triangular wing expanse which is wider cephalad and narrower caudad. The front wings are, therefore, long and narrow while the hind wings are short and broad. This specialization has been accompanied by reduction in the different wing areas.

1. The Fore Wings

The greatest stress to which the wings of insects are subjected is exerted along the distal half of the cephalic margin of the fore wing, where the greatest resistence to the wing is offered by the air. There is, consequently, a need for some special strengthening of this region. This is accomplished in Lepidoptera by the grouping of costa, subcosta, and most, or all, of the branches of radius in a narrow area at the cephalic edge of the wing. Modifications also occur in the structure of the wing scales of this region which stiffen this portion of the wing very materially.

Reduction in the fore wings usually occurs in the anal area. As the hind wings are held in intimate contact with the fore wings, a large development of the anal area would be useless, or even injur-

ious, due to the extensive overlapping which would result. Reduction also occurs in the radial region of some Lepidoptera; while the base of media is atrophied in the non-specialized forms.

Costa:- Costa is figured (Fig. 1) in Comstock and Needham's hypothetical type as an unbranched trachea extending about one-half the distance to the apex of the wing. Spuler omitted it in his figure of the hypothetical type of the primitive lepidopterous venation. All of the pupal wings he figured are of insects in which the costal trachea is minute or wanting. The apparent absence of this trachea led to the belief that costa was not preceded by a pupal wing trachea and,therefore,was not a true vein. Spuler, therefore, considered this vein merely as a thickening of the cephalic margin of the wing. In S. thule, however, the structure of the costal vein and trachea is identical with that of the other veins, leaving no doubt as to the identity of this structure.

In those Lepidoptera studied, there is a considerable amount of variation in the degree of development of the costal trachea. In some cases it is rudimentary, as in Euclea querceti (Fig. 3) and Alypia octomaculata (Fig. 8), while in other cases, particularly in the Saturniidae, it is one of the strongest trachea present in the pupal wing.

In the single wing of Gelechia (Fig. 2) available for study, costa was developed to about the same degree as indicated in the hypothetical wing type. All of the Ceratoeampidae examined had a costal trachea present in the fore wings, although it was not as conspicuous as in the Saturniidae. It is moderately well developed in Basilona imperialis (Fig. 11) and in Citheronia regalis (Fig. 14). In Anisota rubicunda, A. senatoria and A. stigma it is only weakly

developed, although it is always present.

In the Saturniidae, costa is one of the strongest of the pupal wing tracheae. Although there is a certain amount of variation, this trachea never becomes much reduced in this group. This is illustrated by the figures here shown: Antomeris io (Fig. 18), Telea polyphemus (Fig. 22), Tropaea luna (Fig. 26), Callosamia promethea (Fig. 30), Samia rubra (Fig. 32), Samia cecropia (Fig. 35), Rothschildia orizaba (Fig. 44) and Philosamia cynthea (Fig. 47). In the pupal wings of Ampelophaga myron (Fig. 50) costa, although present, is a very weak trachea which follows the course of the costal vein for about a quarter of its length. No trace of the costal trachea was found in the pupal wings of Epargyreus tityrus (Fig. 53) nor of Papilio troilus (Fig. 57) in any of the specimens examined.

Subcosta:- Subcosta is the trachea which lies caudad of costa. In the hypothetical type (Fig. 1) it is two-branched. Spuler figures subcosta with only one branch, and numbers it I, owing to his omission of the costal vein. The fact that subcosta is primarily two-branched is shown by the condition in Stenopis thule, figured by MacGillivray, where two well-developed branches are present. The reason for Spuler's failure to recognize this condition is that the generalized form that he studied, Hepialus sylvinus, did not possess a two-branched subcostal vein.

The first branch of subcosta is lost by atrophy. This is evident when the condition in Stenopis thule is compared with Hepialus. In the former species, Sc_1 is situated at a considerable distance from the tip of Sc_2. It is represented by a comparatively weak trachea, which is sometimes wanting in other species of the genus. This, together with the fact that the subcostal trachea forks so far

proximad of the point of origin of the free part of Sc_1, clearly indicates that this vein is in the process of suppression and leads to the conclusion that the loss is due to atrophy. Complete coalescence is out of the question because of the distance that this branch lies from the tip of Sc_2.

The branch Sc_1 is always wanting in the Frenatae so far as observed. In the figure of the adult wing of _Samia cecropia_ (Fig.33), there is a minute branch developed near the tip of Sc_2. This is undoubtedly a secondary development, as none of the other cecropia wings examined possessed a similar structure.

No instance was found in which the trachea Sc_2 was wanting or even noticeably reduced in any of the pupal wings studied. This trachea was, without exception, one of the strongest tracheae present in the fore wing. The following figures illustrate the condition of the subcostal trachea:- _Gelechia sp._ (Fig. 2), _Euclea querceti_ (Fig. 3), _Alypia octomaculata_ (Fig. 8), _Basilona imperialis_ (Fig. 11), _Samia rubra_ (Fig. 32), _Ampelophaga myron_ (Fig. 50), _Epargyreus tityrus_ (Fig. 53) and _Papilio troilus_ (Fig. 57).

The Radius:- The third main trachea,according to Comstock and Needham's hypothetical type (Fig. 1),and the second,according to Spuler's,is radius, which is typically five-branched. It divides first into an unbranched trachea, R_1,and a stem, the radial sector, which divided dichotomously to give two branches R_{2+3} and R_{4+5} which in turn divide dichotomously to form four branches, R_2, R_3, R_4 and R_5. This method of dichotomy is usually modified in the Lepidoptera. Although many of those wings studied possess a five-branched radius, yet a very few of them followed this typical plan. The greatest amount of reduction among the forms studied was observed in the Sat-

urniidae and Ceratocampidae. In the former radius frquently has but three branches.

The fact that the base of media is wanting in most Lepidoptera obscures the branching of the radial vein, because either the first, or the first and second branches of media are attached to the radial stem by the radio-medial cross-vein. This makes these branches of media appear as branches of the radial vein. The relation of these branches to radius will be discussed under the head of media.

There are five branches to radius in Euclea querceti (Fig. 3) but the typical dichotomy has been lost. It is interesting to note that the branching of the trachea takes place,in this species,within the body of the insect. The only exception found is in the case of the third and fourth branches,which are united until within a short distance of the fork of the veins R_3 and R_4. All the tracheae, however, follow the cavity of the radial vein, and are wound around each other in an irregular,loose coil.

The radial trachea, which is five-branched, in Alypea octomaculata (Fig. 7) is only slightly modified from the hypothetical type. As may be noted, the veins R_3 and R_4 anastomose for a portion of their length, dividing the cell R_3 into two parts. The trachea follow the course of these branches of the vein and lie adjacent in the same vein cavity, R_{3+4}, for a portion of their length, proving the homology of the branches. This is an intermediate step in the complete suppression of the typical dichotomy of the radial sector in certain Lepidoptera. The loss of this cross-vein-like portion of R_3, either by its migration to the first fork of the radial sector,or by its atrophy, completes the destruction of the typical dichotomy. The former is the method by which the proximal portion of R_3 is removed,

because intermediate steps may be found in the adult wing venation. The figure of Datana ministra (Fig. 63) illustrates the condition which follows this; radius is still five-branched, but the branches do not arise according to the typical dichotomy.

Reduction has taken place in the radial area in the Ceratocampidae, and the radial trachea has followed the specialization of the wing veins. This condition is due to the suppression of a stage in the ontogeny of the insect and indicates that the loss of the missing branch of radius occurred long ago in the history of the race. As a result, the study of the radial trachea does not aid in the determination of the homology of the branches of the radial vein.

The only manner in which the homology of the branches of radius may be determined is through a comparative study of the wing veins of members of this and closely related groups. In the Lepidoptera, reduction may take place either by the atrophy or by the coalescence of the veins concerned. The latter seems to be the case in this instance, R_3 and R_4 being the branches uniting.

There are several ways in which this reduction might occur. Comstock, in his Manual for the Study of Insects, indicates that this reduction is due to the atrophy of the second branch of radius. This conclusion is probably reached because of the tendency toward atrophy which occurs in some of the radial branches of the Saturniina. It is, however, very difficult to prove that the second branch is the branch that is atrophied.

Enderlein considers that the reduction which occurs in the Saturniidae is due to the coalescence of R_4 and R_5 with M_1. This is, of course, out of the question as it would be impossible to account for the four-branched condition in the Ceratocampidae if this were

the solution of the problem. Spuler does not figure any wings of the Saturniidae.

Reduction in the radius occurs in other groups of the Lepidoptera by the coalescence of R_2 and R_3, R_3 and R_4, and R_4 and R_5. The most frequent of these is the coalescence of $R_3$and R_4. The only instances of the coalescence of R_2 and R_3 are found in the Sphingidae, Lacosomidae and Lasiocampidae. The coalescence of R_4 and R_5 takes place in many Tineina and is nearly reached in certain of the Arctiidae.

The Saturniina were separated from the remainder of the Lepidoptera quite a long time ago. This is proved by the uniform absence of at least one branch of radius with no indication in the ontogeny as to the manner in which this reduction occurred. They are not closely related to any of those families which indicate a tendency toward the coalescence of R_2 and R_3. The nearest of these, the Sphingidae, separated from the main stem even earlier than did the Saturniidae so that there has been abundant opportunity for the reduction of radius to proceed along diverse lines of specialization. This group is not close to the Tineina and the tendency toward the coalescence of R_3 and R_4 is about as strong as towards the coalescence of R_4 and R_5 as in Arctiidae.

Proof is lacking, at present, as to the method of the reduction of the number of branches of radius. It seems, however, that it is more characteristic of the Lepidoptera for the reduction of radius to occur by the coalescence of R_3 and R_4 than in any other way. This tendency is probably due to the anastomosis of $R_3$and R_4, which,as has already been shown, causes the suppression of the typical dichotomy of radius. The completion of the anastomosis of the proximal portions of these branches leaves the free parts of R_3 and R_4 the short-

est of the branches of radius. R_3 and R_4 are, therefore, most likely to coalesce in the Lepidoptera because this coalescence is already well under way. Until stronger evidence is advanced that the reduction in the number of branches of radius has occurred in some other way, it would seem best to consider that the reduction has taken place by the coalescence of $R_3$and R_4.

Further reduction of radius occurs in the Saturniidae where the reduction is caused by the atrophy of the free part of R_2. That this loss occurs by atrophy is proved by the condition in Samia cecropia. Here individuals are found with the radius consisting of four branches while others have but three. This free part is far enough from the tip of the wing so that it is impossible to consider this loss as due to coalescence. A number of wings were examined with the following result: Radius four-branched, seven; radius three-branched, sixteen. The same condition was observed in Callosamia angulifera,but no data was collected, as the number of wings examined was small. In Telea polyphemus (Fig. 20) the reduction is complete and all the adults had a radius with only three branches, in all the specimens examined.

In the Ceratocampidae, the radial trachea is reduced even further than the radial vein. In the adult wing of Citheronia regalis (Fig. 12) the radial vein is four-branched. In the pupal wing, however (Fig. 14), the radial trachea has but three branches. The same condition occurs in Anisota where the wings have four-branched radial veins and three-branched radial tracheae.

In the Saturniidae also, there are usually fewer branches to the radial trachea than to the radial vein of the same species. Owing to the abundance of material a more thorough study was made in the

case of Samia cecropia than in the other members of the family; and the number of tracheal branches present was found to be variable.

In all the specimens of this species examined, the cephalic branches of radius were found to be weaker than those caudal. The greatest amount of variation in these tracheae is found in R_1, which is completely wanting in some specimens (Fig. 35) although this is rather an unusual condition. R_{3+4} is always weaker than R_5, although this may not be conspicuous in some cases (Fig. 38), in others it is very pronounced (Fig. 35).

It is interesting to note that the reduction of the trachea occurs before the corresponding reduction in the vein takes place. This is true in Citheronia regalis where there is a four-branched vein and a three-branched trachea. It is true in Samia cecropia where the vein has either three or four branches while the trachea has but two or three. Further reduction in the radial vein of this species seems under way, as the basal portion of R_1 is atrophied, leaving it unconnected with the radial stem.

In the only member of the Sphingidae examined, A. myron (Fig. 52), radius is four-branched in both the adult wing veins and in the pupal wing tracheae. The reduction, which has occurred, has taken place through the coalescence of R_2 and R_3. This must be determined by a comparative study of the members of this family, as the tracheae are reduced to the same condition as are the veins. In Hemaris thysbe the branches R_2 and R_3 are not completely fused, thus illustrating the manner in which the reduction of radius has taken place in this family.

An entirely different line of specialization occurs in the front wings of the butterflies, as was pointed out by Headlee. There is a

splitting-back of R_{4+5} so that it arises from the radial stem very close to the base of the wing. This is characteristic of all the butterflies.

The proximal portion of the vein R_{4+5} is atrophied in the adult wings. There is a scar on the radial stem near the proximal end of the discal cell and another just below the distal end of the same, ~~all of~~ which indicates the primitive position of the vein (Fig. 55). This is verified by an examination of the pupal wings of *Epargyreus tityrus* (Fig. 53) and *Papilio troilus*(Fig. 57) where the proximal portion of the trachea is retained.

Media:- The trachea and vein caudad of radius is media. Comstock and Needham consider that this vein has four branches, as is shown in the hypothetical type (Fig. 1). Media branches dichotomously to form two main branches, M_{1+2} and M_{3+4}, which again divide to form four branches. Media is connected with radius by the radio-medial cross-vein and with cubitus by the medio-cubital cross-vein. Another cross-vein, the medial, connects the two main branches of media or M_2 and M_3. As these cross-veins are not preceded by tracheae in the nymphal wing, they are not figured in the hypothetical type.

In the Lepidoptera media is never found with more than three branches. Spuler, therefore, does not include a fourth branch in his figure of the lepidopterous type, and makes no attempt to explain the method of reduction. Comstock and Needham considered that the fourth branch of media coalesced with the first branch of cubitus in the Jugatae. This supposition was based on a wing of *Stenopis* in which the cephalic branch of cubitus is again forked. The extra, cephalic branch was supposed to be M_4, which was anastomosed with Cu_1.

In the other members of the Jugatae, the coalescence was supposed to have been completed. This cannot be the case, as is shown by MacGillivray. This condition in the wing studied by Comstock and Needham is an abnormality because practically all the members of this species have Cu_1 unbranched. There is a great deal of variation in the venation of the wings in the Hepialidae, as extra branches to the veins are of frequent occurrence. Consequently, the presence of this extra vein in a single specimen can be of no weight in deciding what has become of the fourth branch of media. There can be no doubt but that both the trachea and the vein normally have only three branches in all members of the Lepidoptera.

The reduction of media is probably accomplished by the complete coalescence of M_3 and M_4. The homology of the cephalic branches is proved by the location of the medial cross-vein, and by the dichotomy of the trachea. As this cross-vein always connects the second and third branches of media, the two branches cephalad must be M_1 and M_2, because it connects the latter with the caudal branch. This connecting vein must be the medial cross-vein, because it is not preceded by a trachea in any of the wings examined.

Complete proof is wanting as to the manner in which the reduction of the caudal branches takes place. It might occur by the atrophy of either or by the coalescence of the two branches. The latter will be the method which will be assumed to occur in this group.

One of the characteristic modifications of the lepidopterous wing is the atrophy of the proximal portion of media. It is retained by some of the more generalized Lepidoptera, but it is wanting in the great majority of the members of this group. Pupae of none of the species in which the proximal portion of media is retained were

available for study. In those species in which the base of media is strophied, the branches of media are attached to the radial and cubital trunks by the radio-medial and the medio-cubital cross-veins. In many instances, this union is so complete that, on superficial examination, these branches appear to be branches of radius or of cubitus.

An examination of the pupal wings is usually sufficient to remove all doubt of the homology of media, as the proximal portion of the trachea is retained, and the cross-veins are usually not represented by tracheae. In some forms, however, specialization has occurred in the pupal wings and secondary tracheae arising from the radial and cubital trunks have been developed and follow the course of these cross-veins. These secondary tracheae are found developed in many forms scattered through many families; but they are very unusual in generalized Lepidoptera.

The presence of these secondary tracheae is very erratic, only in exceptional cases is an entire family found which possesses them. In the case of *Euclea querceti*, no secondary tracheae were developed, while in *Prolimacodes scapha*, a secondary trachea was developed from radius without exception, among the specimens examined. The Saturniidae is the only family in which all the members examined were found to have this peculiarity. In this case, however, the Ceratocampidae, which are very closely allied to the Saturniidae, did not have secondary tracheae developed in any of the pupal wings examined. In the Nymphalidae, they are present in Anosia but not in Basilarchia *Pieris brassicae* and *P. rapae* are figured by Spuler as possessing well-developed secondary tracheas, but *Papilio*, which belongs in a related family, did not possess them in any of the wings examined.

Spuler, however, includes one of these tracheae in a figure of P. machaon, but it is much reduced in size. These facts show that this condition occurs very widely in many groups, particularly in those more specialized; but that it is nowhere a general development.

The very fact of the irregular distribution of these secondary tracheae and the very high degree of variability which is characteristic of them, practically constitutes proof that they are secondary developments.

If all those forms,which possess these tracheae,were developed from a common ancestor, as would necessarily be the case if they were not secondary in origin, all those Lepidoptera having them should fall into a well-marked group or series of groups,characterised by many common points of similarity. If the attempt were made to include all the species which have this peculiarity in a single group, it would include practically all the Frenatae. Then to account for the absence of these secondary tracheae in the vast majority of the Frenatae, the assumption must be made that they were generally atrophied. As these tracheae are internal organs of little or no possible use in forming a basis for natural selection, it is extremely improbable that such a general atrophy would occur. It would be natural to suppose that those forms which have undergone the least change in form from this hypothetical ancestor would be most likely to possess the character. However, this is not the case. The condition of the tracheae indicates, rather, that there has been a suppression of a stage in the ontogeny of the insect. The condition realized, when these tracheae are developed, is one of greater similarity to the adult wing venation than where they are wanting. It appears, therefore, that the tracheation is assuming the specialization characteristic of the

adult wing venation with the consequent loss of the more generalized tracheation.

It is evident, then, that Enderlein's hypothesis that the trachea developed from radius was R_{4+5} and that the one developed from cubitus precedes the medio-cubital cross-vein cannot be the case, because neither of these two veins are secondary in nature.

Once the secondary nature of these tracheae is understood, it is simple to homologize the medial vein and trachea. In all the species studied,media was three-branched in the adult. This was usually true in the pupal wings, as well; but in a few cases the medial trachea was reduced owing to the development of a secondary trachea. The first branch of media was the only one to atrophy in this manner, as is illustrated by *Samia cecropia* (Fig. 38). This condition is rather rare in the fore wings.

In *Euclea querceti* (Fig. 3), *Alypia octomaculata* (Fig. 8) and in all the Ceratocampidae examined (*Citheronia regalis*, Fig. 14) the medial trachea was three-branched with no secondary tracheae developed. In *Prolimacodes scapha*,media is two-branched, and the atrophied branch, M_1, is replaced by a secondary branch of radius. In most of the wings of the Saturniidae examined,media is three-branched with a secondary trachea developed from radius, and frequently one from cubitus. This condition is found in *Automeris io* (Fig. 18), *Telea polyphemus* (Fig. 22), *Callosamia promethea* (Fig. 30), *Samia rubra* xxx (Fig. 32) and *Samia cecropia* (Fig. 35). In *Samia cecropia* there is a great amount of variation shown in the condition of M_1. In one instance (Fig. 38) this trachea is atrophied.

In *Ampelophaga myron* (Fig. 1), *Epargyreus tityrus* (Fig. 53), and in *Papilio troilus* (Fig. 57) media is three-branched with no indica-

tion of secondary trachea in the wing.

Cubitus:- Cubitus is the trachea next caudad of media. Comstock and Needham, and Spuler figure this trachea as two-branched. In those Lepidoptera studied, cubitus was one of the most constant tracheae found in the pupal wing. The only marked modification is the development of a secondary trachea in the Saturniidae and *Anosia*, as was mentioned above. The cubital trachea was found invariably well-developed, never being materially reduced in size. There is very little variation in the cubital vein in the adult wing.

The condition of cubitus is illustrated by *Euclea querceti* (Fig. 3), *Alypia octomaculata* (Fig. 8), *Basilarchia imperialis* (Fig. 11), *Citheronia regalis*(Fig. 14), *Samia cecropia* (Fig. 37), *Ampelophoga myron* (Fig. 51), *Epargyreus tityrus* (Fig. 53) and *Papilio troilus* (Fig. 57). In none of the above examples is a secondary trachea developed. In another example of *Samia cecropia* (Fig. 35), however, a secondary trachea is found. This is the usual case among saturnians,as is shown by the presence of such a trachea in over three-fourths of the specimens of *S. cecropia* and in practically all of the saturnians examined.

The Anal Area:- In Comstock and Needham's figure of the hypothetical type, the anal tracheae are figured as three unbranched tracheae caudad of cubitus. They are called the first, second, and third anal tracheae (1st A, 2nd A, 3d A). Spuler also figures three anal tracheae, but he shows the third one branched. This condition is characteristic of the Lepidoptera. The names applied by Spuler to these tracheae were V, alpha, and beta, respectively. He made no distinction between the branches of beta, and does not note which is retained in the adult wing.

The first anal vein is wanting in all of the fore wings examined. The trachea, however, is uniformly present; and is at least fairly well-developed, as is shown by the following examples: *Euclea querceti* (Fig. 3), *Alypia octomaculata* (Fig. 8), *Basilona imperialis* (Fig. *Samia rubra* (Fig. 32), *Epargyreus tityrus* (Fig. 53) and *Papilio troilus* (Fig. 57).

The second anal vein is present in all the species examined. The trachea which precedes this vein is the strongest of the anal tracheae. It is present in all the specimens examined and is illustrated by the figures listed above.

The third anal trachea was branched in a majority of the pupal wings examined, as was pointed out by Spuler. Enderlein found a similar condition in the pupal wings that he studied and named these tracheae the axillaries. There can be no doubt, however, that the axillaries are homologous with the third anal trachea of Comstock and Needham, the only modification is the presence of two branches instead of one. Their point of origin and position in the wing is identical with that of the third anal trachea. Enderlein figures his axillaries as arising independently and this condition was found in several instances. In the majority of cases, however, the main stem of the third anal trachea is present, usually extending well into the wing before branching occurs.

The first branch of the third anal vein was found in a majority of the adult wings examined, and was coalesced with the second anal vein for the greater part of its length, only a comparatively small portion of the proximal end is free. The tracheation of the pupal wing also indicates this coalescence with the second anal vein(Figs. 3, 8, 50, and 53). The first branch of the third anal trachea fol-

lows the vein cavity of the second anal vein after passing through the basal portion of the vein which it represents.

It seems likely, however, that there are two lines of specialization in the wings of Lepidoptera. In the moths, at least, it seems that the coalescence of these two veins may take place even when the distal portion of the first anal trachea lies at a considerable distance from the second anal trachea. This is true in the Saturniidae as is shown in the adult (Fig. 43) and pupal wings (Fig. 44) of Rothschildia orizaba. The proximal portion of the first branch of the third anal trachea is represented by a vein which coalesces with the second anal vein, while the distal portion of this trachea does not approximate the position of the second anal trachea. As this is connected by intermediate forms with others in the group in which there can be no doubt of the homology, it seems likely that where only a single vein is retained in the adult wing it is probably the second anal and the first branch of the third in which coalescence has become complete. This tendency is indicated by the manner in which the proximal portions of the two veins draw together and the point of union migrates towards the base of the wing.

In Papilio (Fig. 57) there seems to be another line of development. Here both the vein and trachea of the first branch of the th third anal arise from the proximal end of the second anal vein. The distal portion of the vein curves strongly caudad and terminates at the caudal margin of the wing. The trachea turns and extends along the caudal margin to the anal angle of the wing. Owing to the lack of material it is not possible to determine if this line of development is characteristic of the butterflies.

The second branch of the third anal vein is wanting in the adult

wings of practically all Lepidoptera. The loss of this vein has been due to atrophy, as is shown by the continued presence of the trachea while no vein is formed around it. It is always a weak trachea which extends along the caudal margin of the wing in much the same manner that costa follows the cephalic margin. The second branch of the third anal trachea is represented in *Euclea querceti* (Fig. 3), *Alypea octomaculata* (Fig. 8), *Citheronia regalis* (Fig. 14), *Telea polyphemus* (Fig. 22), *Samia cecropia* (Fig. 39), *Rothschildia orizaba* (Fig. 44), *Ampelophaga myron* (Fig. 50), *Epargyreus tityrus* (Fig. 53), and *Papilio troilus* (Fig. 57). This trachea was found to be present in at least one example whenever a considerable series of specimens of any single species was examined. This indicates that it is characteristic of the Lepidoptera.

In addition to the two branches of the third anal trachea that are normally present in the pupal wing, secondary tracheae are frequently developed. They have the appearance of the normal branches of the third anal trachea and are attached either to the main stem or the second branch. They are usually quite weak. The lack of uniformity in their point of origin and course, even in the two wings of the same individual, proves that they are merely secondary in character.

2. The Hind Wings

The specialization found in the hind wings of the Frenatae is quite different from that of the fore wings. In the generalized forms, the Jugatae, in which little progress has been made toward the formation of a triangular wing expanse, there is little difference in venation between the two wings. This similarity is shown by Spuler's hypothetical figure for the venation of the Lepidoptera.

The only differences indicated by him are the presence of a short spur arising from the base of subcosta (I) which is wanting in his figure of the front wings. He also omits the second branch of the third anal trachea (beta) which he figures in the fore wing. The latter trachea should be included in the scheme of the hind wings, as will be shown later.

Spuler's figure exemplifies the generalized venation of the Jugatae, as may be seen by a comparison with Stenopis thule as figured by MacGillivray. The chief difference between the two is the absence of the first branch of subcosta in the type and its presence in the wing of Stenopis. Among the generalized forms, the hind wing is only slightly modified from the general plan of the fore wing, as is illustrated by Spuler's figure.

Costa:- The costal vein is present in all wings along the cephalic margin. In a majority of cases it is not strongly chitinized and is difficult to identify. However, it is just as characteristic of the hind wings as of the fore, as is shown by the presence of a costal trachea in the pupal wings. As the costal margin of the hind wing is supported by the anal area of the fore wing, there is no need of a strong vein along the edge of the wing, and a strong vein would tend to reduce the flexibility of the wing area and thus impair its value as an organ of flight. This undoubtedly accounts for the reduction of the costal vein.

MacGillivray figures a chitinized costal vein as present in the pupal wing of Stenopis thule; but no trachea was observed as preceding it. The costal trachea is frequently reduced or apparently wanting, as would be expected in consideration of the usual reduction of this vein in the adult wing.

The costal trachea is present in some specimens of Euclea querceti (Fig. 4) and Prolimacodes scapha (Fig. 6) extending cephalad from the base of subcosta. It is never strongly developed, and in many instances is apparently wanting. A very similar condition is found in the wings of Alypia octomaculata in which the trachea is a trifle stronger and considerably longer. It is of more general occurrence in these wings, and is bent distad along the cephalic margin of the wing.

A rather weak costal trachea is characteristic of the Ceratocampidae (Fig. 15), while in the Saturniidae, it is strongly developed (Figs. 23, 40). A rather weak trachea, extending along the cephalic margin of the wing is present in Ampelophaga myron (Fig. 52). No costal trachea was found in the wings of Epargyreus tityrus, but a small trachea was observed in the wings of Papilio troilus.

Subcosta:- The subcostal vein is two-branched in certain of the Jugatae, as is the case in the fore wings. This was shown by MacGillivray in the instance of Stenopis thule, where the first branch of subcosta occurs. It is preceded by a trachea in the pupal wings, but this trachea does not extend into the free part of Sc_1, so far as observed. The reduction of the first branch occurs by the atrophy of the free part, as is indicated by the inconstancy of this vein. The distance of the point of origin of the free part of Sc_1 from the tip of Sc_2 is so great that coalescence is very improbable.

The second branch of subcosta is as constant in the hind as in the fore wings; and is represented by a very strong trachea in all the specimens examined. The condition of subcosta is illustrated by the following figures: Euclea querceti (Fig. 4), Alypia octomaculata (Fig. 10), Citheronia regalis (Fig. 15), Telea polyphemus (Fig.

33), Samia cecropia (Fig. 40), Ampelophaga myron (Fig. 53), Epargyreus tityrus (Fig. 54), and Papilio troilus (Fig. 59)

The area cephalad of subcosta is usually expanded to furnish an area which will extend forward beneath the front wings to ensure coordination of movement essential in flight. In the moths this area is rarely furnished with veins, as it is held in position by the jugum or frenulum as the case may be. The only vein, in those cases where the frenulum is developed, is a thickening of the costal margin of the wing extending from the base of the wing to the frenulum. This vein is costa without a doubt.

In most of the butterflies and in the Lasiocampidae, among the moths, the frenulum is atrophied, while a greatly expanded area is developed. Some support must be given to this area or it would not have the stiffness necessary to hold it in place. This is accomplished by the production of secondary veins. In Comstock's Manual, these veins in the Lasiocampidae are called humeral veins, while the spurs in the butterflies, which are apparently identical, are called costa, I.

No pupal wings of any of the Lasiocampidae were available for examination, but it is evident that the spur present in Papilio troilus cannot be the costal vein. In Figure 61, costa is represented as a very weak trachea extending cephalad along the proximal margin of the wing. A similar condition existed in the specimen shown in Figure 60, but the costal trachea does not appear in the photograph, owing to that portion of the wing being out of focus.

The subcostal trachea is the well developed trachea extending to the apical angle of the wing. It branches near its base and gives rise to a trachea which extends along and beyond the spur developed from the base of subcosta.

This trachea cannot be homologous with costa because it is not found in the position normally occupied by that trachea, while another trachea does exist in the wing which, as was shown above, is homologous with costa in other wings. It cannot be the first branch of subcosta because that vein and trachea is atrophied in most of the generalized forms, and no intermediate forms, in which Sc_1 is present, exist. This trachea cannot represent the humeral cross-vein because cross-veins are not preceded by tracheae; so that even if the vein in the adult wing were the humeral cross-vein, this trachea would be, necessarily, secondary in nature. It is possible that the butterflies are developed along a line that has retained the humeral cross-vein, but it would be difficult to understand how there could be two humeral cross-veins as in the Lasiocampidae. In the latter case, both veins must be secondary, as none of the relatives of this group have such veins. It seems likely that this vein is secondary in the butterflies as well, because of the usual absence of a humeral cross-vein in more generalized forms.

Radius:- Radius is five-branched in the Jugatae as is shown by Stenopis figured by MacGillivray. It is practically identical with this vein in the fore wing of the same suborder.

In the Frenatae, however, a considerable reduction has occurred in this vein; only two branches are retained. Comstock, in the Manual for the Study of Insects, considered the radius as consisting of a single branch. He overlooked the first branch, which is coalesced with subcosta for most of its length. Spuler had already pointed out this condition in his paper on the phylogeny and ontogeny of the wing veins of the Lepidoptera. There can be no doubt of the homology of this cephalic branch of radius when the pupal wings are

examined. Only very specialized forms have this trachea wanting, even in those cases where the cross-vein-like portion of the vein has migrated to the base of the wing, and is apparently wanting the trachea persists.

There is little variation usually found in the radial trachea. Both the vein and trachea are two-branched in Euclea querceti (Fig. 4) and Alypia octomaculata (Fig. 10). The proximal cross-vein-like portion of the vein has migrated to the base of the wing in Citheronia regalis (Figs. 13 and 15), Automeris io (Figs. 17 and 19), Telea polyphemus (Figs. 21 and 23), Tropaea luna (Fig. 29) and Philosamia cynthia (Figs. 48 and 49), and the trachea R_1 has been retained in the wing. In Samia cecropia (Fig. 40), Callosamia promethea (Fig. 31) and Rothschildia orizaba (Fig. 46), the cephalic branch of the trachea is atrophied. It is almost certain that R_1 is not always present in those forms listed above and not always absent in the others.

In Ampelophaga myron (Fig. 52), Epargyreus tityrus (Fig. 54) and Papilio troilus (Fig. 60) this trachea is retained as is the proximal portion of the vein which it represents. The radial trachea frequently gives rise to secondary tracheae which supplant the normal branches of media, as in the fore wing.

Media:- The condition in media is identical to that in the fore wing. The basal portion of the vein is atrophied in all but the most generalized forms, and the branches are attached to radius and cubitus by the radio-medial and the medio-cubital cross-veins. The trachea retains its proximal portion and usually all of its branches, but secondary tracheae may take the place of one or even two of these branches. The homology is easily determined, however,

by a comparison with the fore wings.

The three branches of the medial trachea are separate to the base of the wing in *Euclea querceti* (Fig. 4) as in the front wing. In *Prolimacodes scapha* (Fig. 5), the first branch of the medial trachea is wanting, its place being taken by a secondary branch of radius. Media is branched normally in *Alypia octomaculata* (Fig. 8), and the medial cross-vein is wanting. In *Citheronia regalis* (Fig. 15), media is three-branched with no secondary tracheae developed from either radius or cubitus, while in *Automeris io* (Fig. 19), *Telea polyphemus* (Fig. 23), *Tropaea luna* (Fig. 29), *Callosamia promethea* (Fig. 31), *Samia cecropia* (Fig. 40), *Rothschildia orizaba* (Fig. 45), and *Philosamia cynthia* (Fig. 49) of the Saturniidae, there are secondary trachea present in this area. In *Ampelophaga myron* (Fig. 52), *Epargyreus tityrus* (Fig. 54) and *Papilio troilus* (Fig. 59), media is three-branched with no secondary tracheae developed.

Cubitus:- Cubitus is invariably two-branched in the hind wings; both veins and tracheae are well-developed with only slight variations. Cubitus is illustrated by the following figures: *Euclea querceti* (Fig. 4), *Alypia octomaculata* (Fig. 10), *Citheronia regalis* (Fig. 15), *Telea polyphemus* (Fig. 23), *Samia cecropia* (Fig. 40), *Philosamia cynthea* (Fig. 49), *Ampelophaga myron* (Fig. 52), *Epargyreus tityrus* (Fig. 54) and *Papilio troilus* (Fig. 59).

Anal Area:- The anal area of the hind wings of Lepidoptera is usually not so reduced as is this region in the front wings. There is a considerable amount of variability in this regard, however, as is shown by the material studied. *Euclea querceti* and *Prolimacodes scapha* have three anal veins, *Alypia octomaculata* and *Citheronia regalis* but two, the Saturniidae only one, *Ampelophaga myron* and *Epar-*

gyreus tityrus two, and *Papilio troilus* one. In the pupal wing, there are three well-developed tracheae, no matter how many of the veins are atrophied in the adult wing. The two cephalic tracheae are always unbranched, but the third frequently has a small branch extending caudad from its proximal portion. As in the fore wing, this caudal trachea is usually not followed by a vein. Comstock (in Beutenmuller's Monograph of the Sesiidae) considers that where a fourth anal vein is present in the hind wing, as is the case with some members of this group, the third anal vein is branched. The frequent presence of the weakly developed trachea representing the second branch of the third anal trachea proves that the third anal vein is developed around the first branch of the third anal trachea. Although the number of veins is not constant, the number of tracheae is very uniform; the greatest variability is shown in regard to the presence of the second branch of the third anal trachea. Where atrophy of one of the three anal veins occurs, it is invariably the first that is wanting. The second vein to disappear is the first branch of the third. When but one vein is retained, it is invariably the second.

The condition in the anal area is illustrated by the following figures: *Euglea querceti* (Fig. 4), *Citheronia regalis* (Fig. 15), *Telea polyphemus* (Figs. 21 and 23), *Tropaea luna* (Fig. 29), *Samia cecropia* (Figs. 34 and 41), *Philosamia cynthia* (Figs. 48 and 49), *Ampelopaga myron* (Fig. 52), and *Papilio troilus* (Fig. 59). None of the preceding examples show the second branch of the third anal trachea. In those following, however, this trachea is present: *Prolimacodes scapha* (Fig. 6), *Alypia octomaculata* (Fig. 10), *Automeris io* (Fig. 19), *Telea polyphemus* (Fig. 24), *Samia cecropia* (Figs. 40 and 42) and *Rothschildia orizaba* (Fig. 45). Some names appear in both

lists, indicating the high degree of variability that occurs in this trachea. It is likely that other names would be found in both lists, if a greater number of specimens were examined.

IV MODIFICATIONS OF THE TRACHEATION

One of the most conspicuous characteristics of the tracheation of the pupal wings studied was the high degree of variability found in many of the species. The degree to which variation occurred was not constant in the different groups, the butterflies and the more generalized moths were more constant, as a rule, than the more specialized moths, as the Saturniidae. Those species in which there had been considerable modification of the tracheation exhibited the greatest amount of variation.

The variations of most general occurrence may be divided as follows: The splitting-back of the tracheal branches of the main tracheae, thus eliminating the main trunk of the trachea in certain cases, the union of two tracheal trunks which are normally separate, the development of secondary tracheae; and the atrophy of a trachea which is normally present in the wing.

The splitting-back of the branches of the tracheae of the pupal wing is characteristic of <u>Euclea querceti</u>, in particular, although it is found in many groups. In this species (Figs. 3 and 4), practically all the branches arise in the body cavity, and follow the normal course of the tracheal trunk until they reach the free part of the branch they represent along which they extend. The tracheal trunk is wanting and its place taken by a loose coil of the tracheal branches. The only case in which any branching occurs within the wings of this species, so far as observed, is in the case of R_3 and R_4 which are

united until they are just proximad of the forking of the branches R_3 and R_4.

A very similar condition is found in the wings of Prolimacodes scapha. In this case, however, the splitting-back is not quite so complete as in E. querceti. The secondary trachea arising from radius, which takes the place of the first branch of media, is not free to the base of the wing; but is united to radius at the point of origin of the radio-medial cross-vein. In the hind wing (Fig. 5) the radial stem is present, as is usually the case in the pupae. In the fore wing, radius sometimes has as few as two trachea present in the stem of radius. The medial stem is sometimes undivided.

In Sanninoidea exitosa the splitting-back is usually complete, as is figured in Bentenmuller's Monograph of the Sesiidae. Isolated examples are also found in other groups, but the splitting-back is not so complete as in the examples mentioned above. In some specimens of Basilona imperialis R_1 is separate from R_s, in Automeris io M_{1+2} is separate from M_{3+4} and cubitus is split clear to the base, and in Samia cecropia (Fig. 42) cubitus is split back to the base of the wing.

In a few individuals in the Saturniidae the first anal trachea is fused with the cubital trunk for some distance from the base of the wing. This is illustrated by Figure 39 of the fore wing of Samia cecropia.

This union of the tracheal trunks is clearly a more specialized condition than where they are free, as is normally the case. It seems likely, then, that the splitting-back is a more generalized condition than is the normal condition. If this is the case, it seems likely that this may represent a more generalized condition than that

figured by Comstock and Needham in their hypothetical type of wing tracheation. The tendency seems to be for the tracheation to follow the specialization of the veins, so that the condition illustrated by the hypothetical type would naturally result from a type in which the trachea are split back to the base of the wing.

The development of secondary tracheae may occur from the branches of radius and cubitus, as was shown in the previous pages. In such instances they illustrate the tendency of the tracheation to follow the specialization of the veins. In other cases they originate from the base of the wing, in which case they have no significance except to show that variation is of more general occurrence in the tracheation than in the venation of the wings. Examples of this development of secondary tracheae from the base of the wing are shown by Figures 14 and 49.

The atrophy of a trachea, which is represented by a vein in the adult wing, is of rather frequent occurrence in the Saturniidae. In Samia cecropia, for example, the trachea representing R_1 is frequently atrophied, as was shown on a previous page. It ~~has~~ was ~~been~~ pointed out at that time that this condition indicates that the vein represented by such a trachea is in the process of suppression.

V SUMMARY

In the preceding discussion an attempt has been made to prove the following points:

1. The co-called splitting-back of the tracheae in Euclea querceti, et al., indicates a more generalized tracheation than that found in the hypothetical type of Comstock and Needham.

2. The splitting-back of R_{4+5} in the Rhopalocera indicates a generalized rather than a specialized condition.

3. The coalescence of the tracheal trunks may occur in specialized forms, as illustrated by the cubital and the first anal trachea.

4. The loss of a tracheal branch may precede the loss of the vein which is usually formed around it.

5. The tracheae developed from radius and from cubitus which were described by Enderlein as R_{4+5} and the medio-cubital cross-vein, respectively, are secondary in origin.

6. The tendency exists for the tracheation to follow the specialization of the venation with the consequent suppression of some of the stages in the ontogeny.

7. The reduction characteristic of the radial area of the Saturniina is accomplished by the coalescence of R_3 and R_4.

8. The spur which is characteristic of the humeral area of certain Heterocera and Rhopalocera is secondary in origin.

9. The third anal trachea of the hind wings of the Lepidoptera is typically two-branched, as is the case in the fore wings.

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VII EXPLANATION OF PLATES

Plate I

Fig. 1 Hypothetical type of comstock and Needham

Fig. 2 Pupal fore wing of Gelechia sp.

Plate 2

Fig. 3 Pupal fore wing of Euclea querceti

Fig. 4 Pupal hind wing of Euclea querceti

Plate 3

Fig. 5 Pupal hind wing of Prolimacodes scapha

Fig. 6 Basal area of pupal hind wing of Prolimacodes scapha

Plate 4

Fig. 7 Radial area of the pupal fore wing of Alypia octomaculata

Fig. 8 Pupal fore wing of Alypia octomaculata

Plate 5

Fig. 9 Anal area of the pupal hind wing of Alypia octomaculata

Fig. 10 Pupal hind wing of Alypia octomaculata

Plate 6

Fig. 11 Pupal fore wing of Basilona imperialis

Fig. 12 Adult fore wing of Citheronia regalis

Plate 7

Fig. 13 Adult hind wing of Citheronia regalis

Fig. 14 Pupal fore wing of Citheronia regalis

Plate 8

Fig. 15 Pupal hind wing of Citheronia regalis

Fig. 16 Adult fore wing of Automeris io

Plate 9

Fig. 17 Adult hind wing of Automeris io

Fig. 18 Pupal fore wing of Automeris io

Plate 10

Fig. 19 Pupal hind wing of Automeris io

Fig. 20 Adult fore wing of Telea polyphemus

Plate 11

Fig. 21 Adult hind wing of Telea polyphemus

Fig. 22 Pupal fore wing of Telea polyphemus

Plate 12

Fig. 23 Pupal hind wing of Telea polyphemus

Fig. 24 Pupal hind wing of Telea polyphemus

Plate 13

Fig. 25 Adult fore wing of Callosamia angulifera

Fig. 26 Pupal fore wing of Callosamia angulifera

Plate 14

Fig. 27 Pupal hind wing of Callosamia angulifera

Fig. 28 Pupal fore wing of Tropaea luna

Plate 15

Fig. 29 Pupal hind wing of Tropaea lune

Fig. 30 Pupal fore wing of Callosamia promethia

Plate 16

Fig. 31 Pupal hind wing of Callosamia promethia

Fig. 32 Pupal fore wing of Samia rubra

Plate 17

Fig. 33 Adult fore wing of Samia cecropia

Fig. 34 Adult hind wing of Samia cecropia

Plate 18

Fig. 35 Pupal fore wing of Samia cecropia

Fig. 36 Pupal fore wing of Samia cecropia

Plate 19

Fig. 37 Pupal fore wing of Samia cecropia

Fig. 38 Pupal fore wing of Samia cecropia

Plate 20

Fig. 39 Pupal fore wing of Samia cecropia

Fig. 40 Pupal hind wing of Samia cecropia

Plate 21

Fig. 41 Pupal hind wing of Samia cecropia

Fig. 42 Pupal hind wing of Samia cecropia

Plate 22

Fig. 43 Adult fore wing of Rothschildia orizaba

Fig. 44 Pupal fore wing of Rothschildia orizaba

Plate 23

Fig. 45 Pupal hind wing of Rothschildia orizaba

Fig. 46 Pupal hind wing of Rothschildia orizaba

Plate 24

Fig. 47 Pupal fore wing of Philosamia cynthia

Fig. 48 Adult hind wing of Philosamia cynthia

Plate 25

Fig. 49 Pupal hind wing of Philosamia cynthia

Fig. 50 Pupal fore wing of Ampelophaga myron

Plate 26

Fig. 51 Anal area of the pupal hind wing of Ampelophaga myron

Fig. 52 Pupal hind wing of Ampelophaga myron

Plate 27

Fig. 53 Pupal fore wing of Epargyreus tityreus

Fig. 54 Pupal hind wing of Epargyreus tityreus

Plate 28

Fig. 55 Adult fore wing of Papilio turnus

Fig. 56 Adult hind wing of Papilio turnus

Plate 29

Fig. 57 Pupal fore wing of Papilio troilus

Fig. 58 Basal portion of the pupal fore wing of Papilio troilus

Plate 30

Fig. 59 Pupal hind wing of Papilio troilus

Fig. 60 Humeral area of the pupal hind wing of Papilio troilus

Plate 31

Fig. 61 Pupal hind wing of Papilio troilus

Fig. 62 Humeral area of the pupal hind wing of Papilio troilus

Plate 32

Fig. 63 Pupal fore wing of Datana ministra

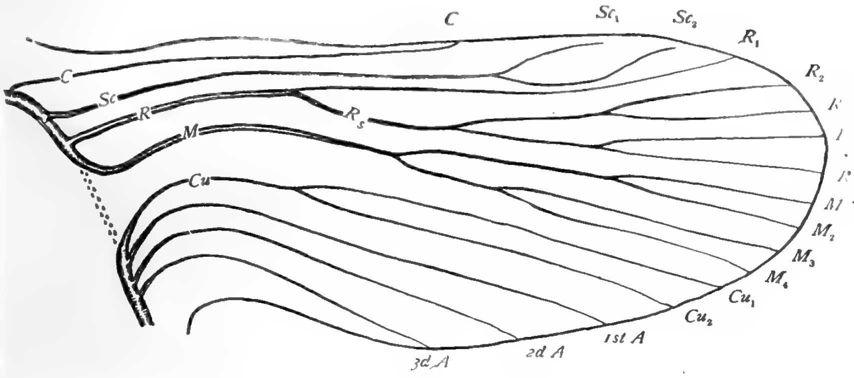
Fig. 64 Spuler's scheme of the tracheation of the primitive lepidopterous wing

Plate 33

Fig. 65 Pupal fore wing of Hepialus thule, after MacGillivray

Fig. 66 Pupal hind wing of Hepialus thule, after MacGillivray

Plate 1



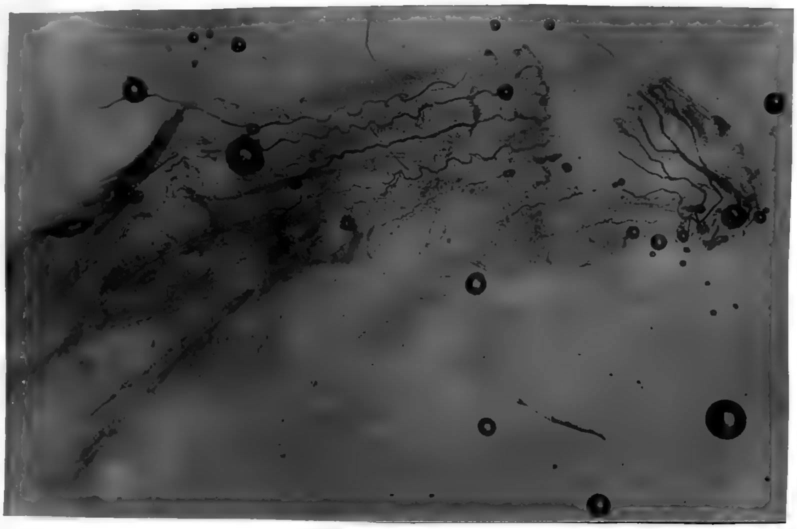
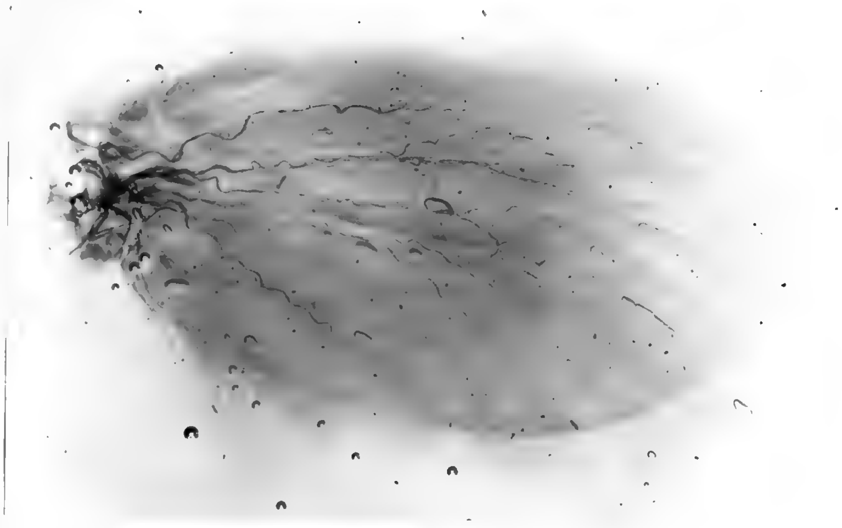


Fig. 1 Hypothetical type of Comstock and Needham

Fig. 2 Pupal fore wing of Gelechia sp.

Plate 2



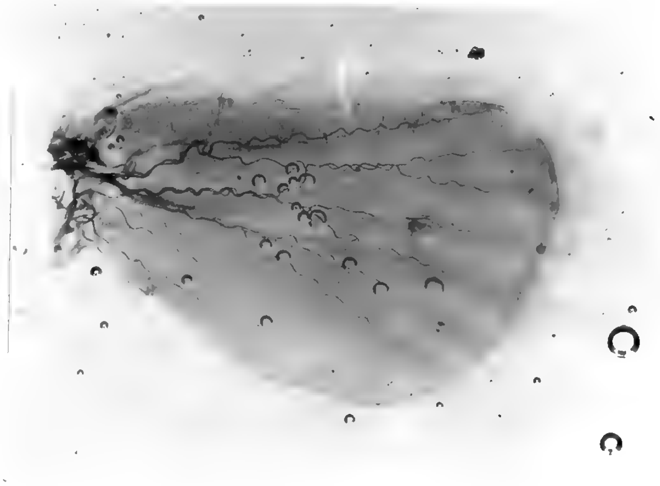


Fig. 3 Pupal fore wing of Euclea querceti

Fig. 4 Pupal hind wing of Euclea querceti

Plate 3

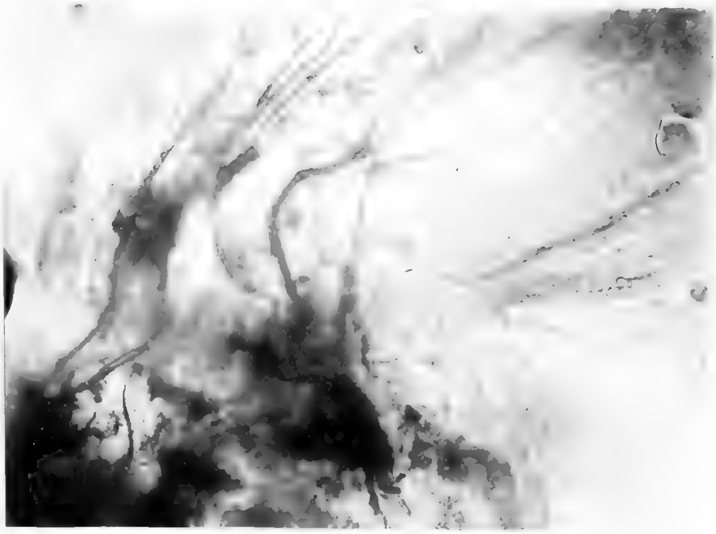


Fig. 5 Pupal hind wing of Prolimacodes scapha

Fig. 6 Basal area of pupal hind wing of Prolimacodes scapha

Plate 4

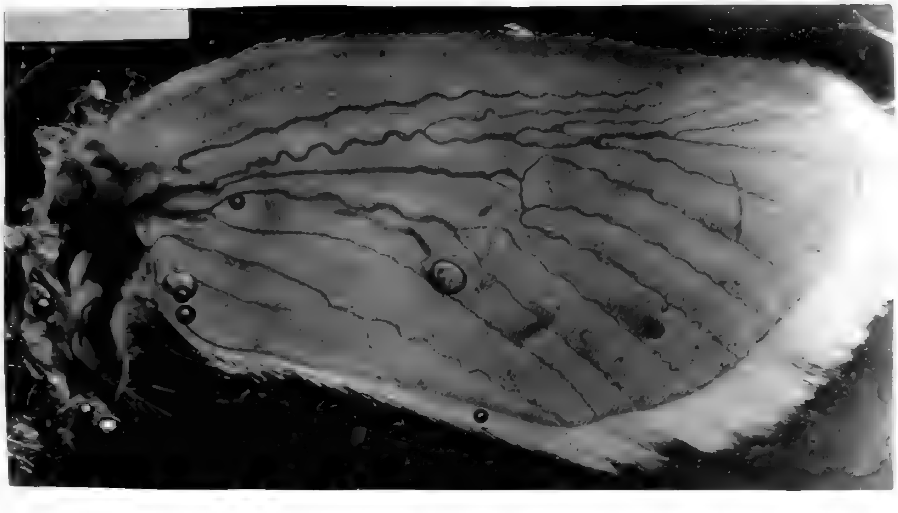


Fig. 7 Radial area of the pupal fore wing of Alypia octomaculata

Fig. 8 Pupal fore wing of Alypia octomaculata

Plate 5

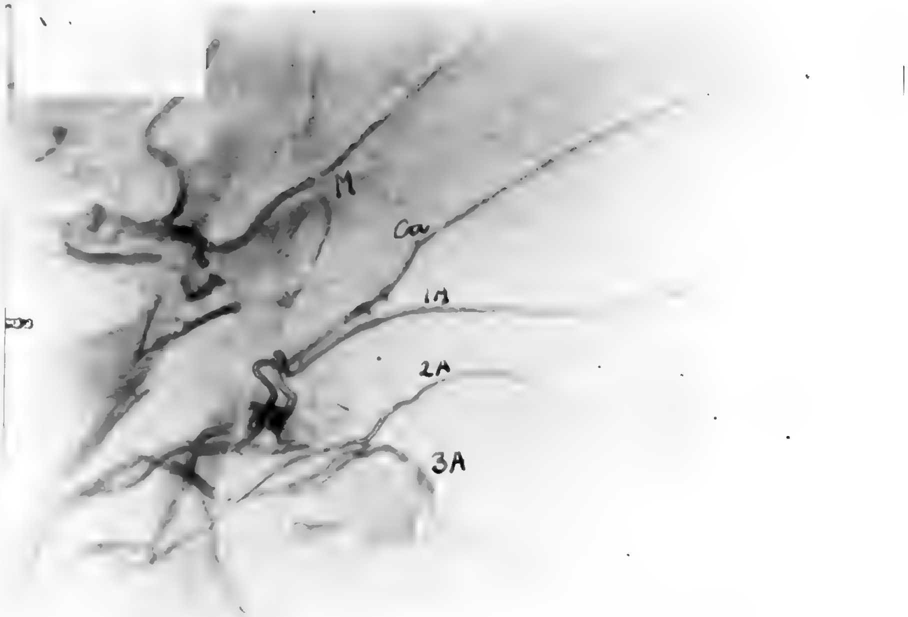


Fig. 9 Anal area of the pupal hind wing of Alypia octomaculata

Fig. 10 Pupal hind wing of Alypia octomaculata

Plate 6

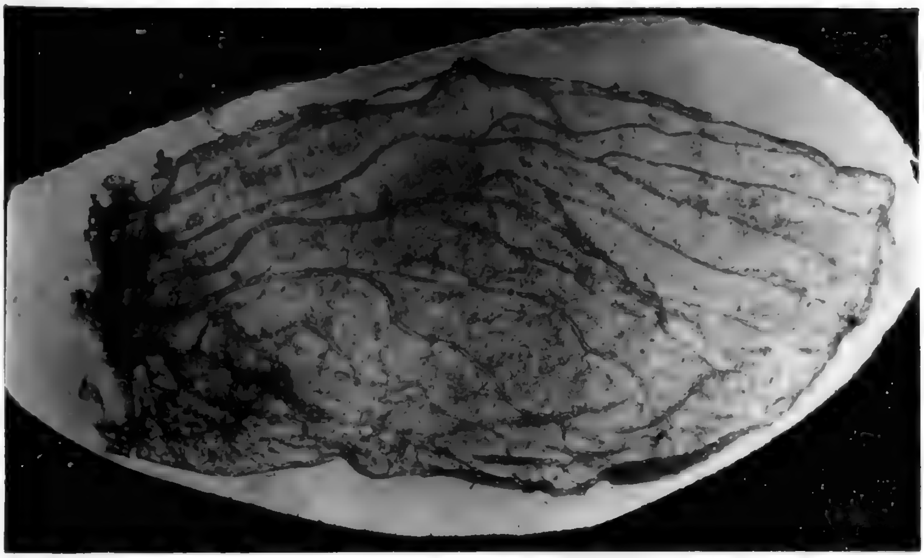
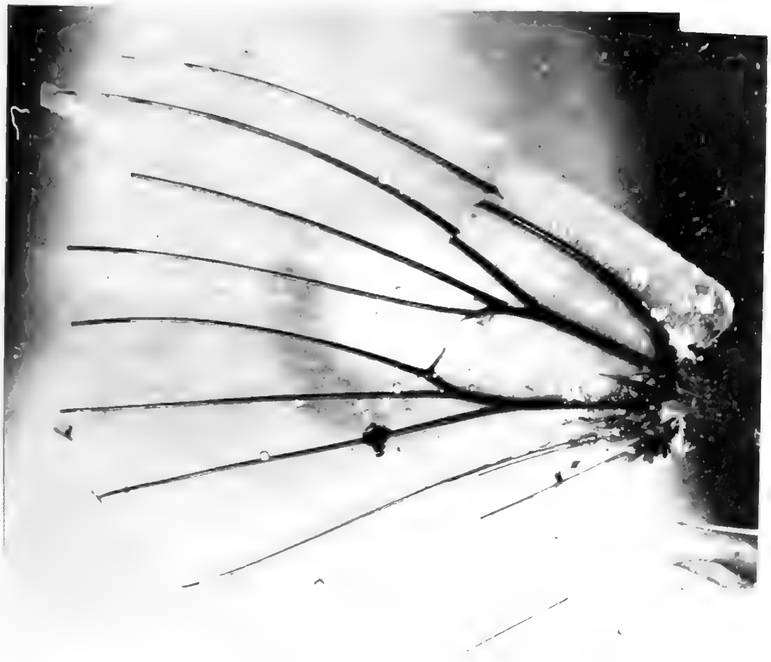


Fig. 11 Pupal fore wing of Basilona imperialis

Fig. 12 Adult fore wing of Citheronia regalis

Plate 7



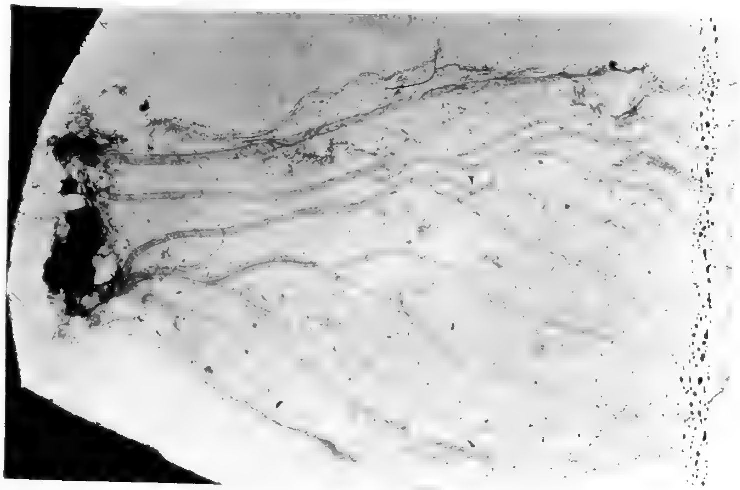


Fig. 13 Adult hind wing of Citheronia regalis

Fig. 14 Pupal fore wing of Citheronia regalis

Plate 8

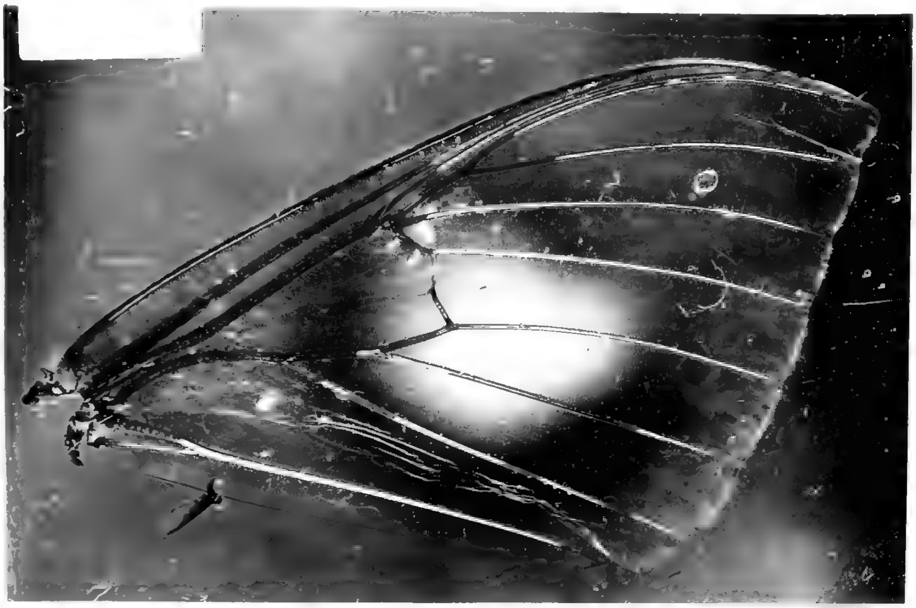
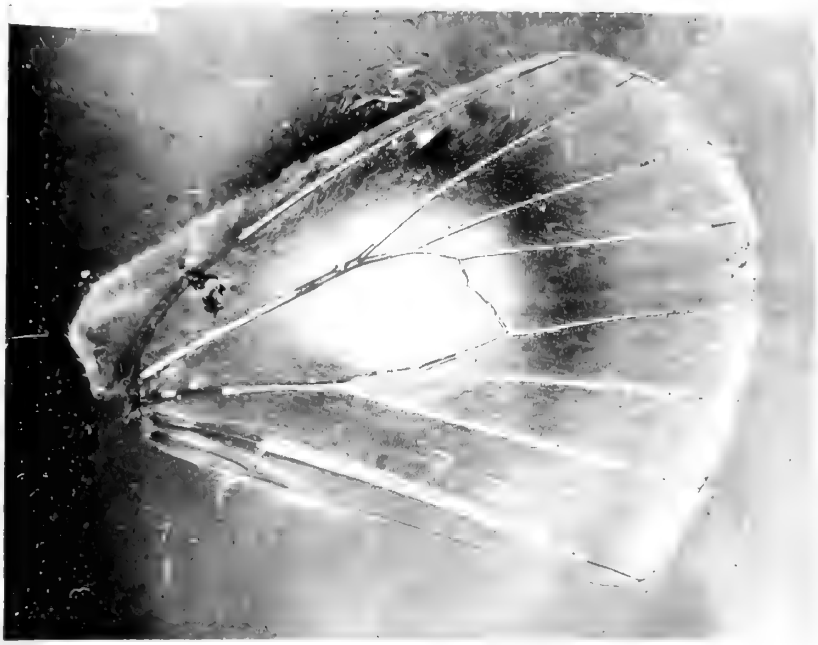


Fig. 15 Pupal hind wing of Citheronia regalis

Fig. 16 Adult fore wing of Automeris io

Plate 9



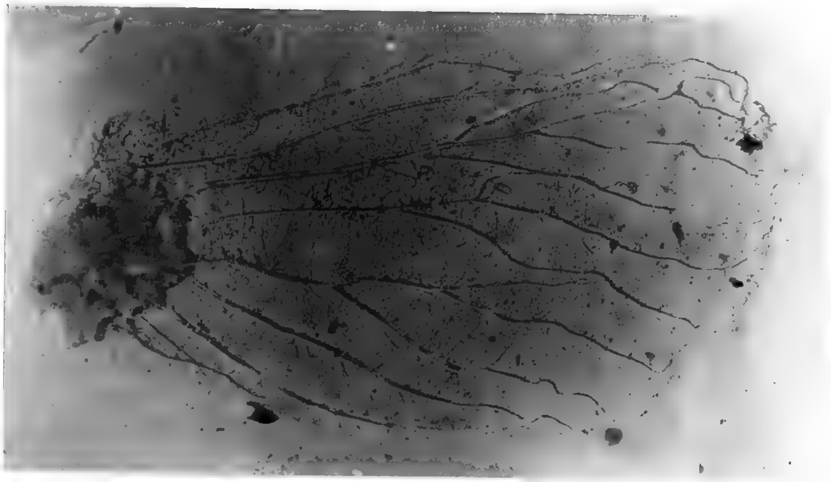


Fig. 17 Adult hind wing of Automeris io

Fig. 18 Pupal fore wing of Automeris io

Plate 10

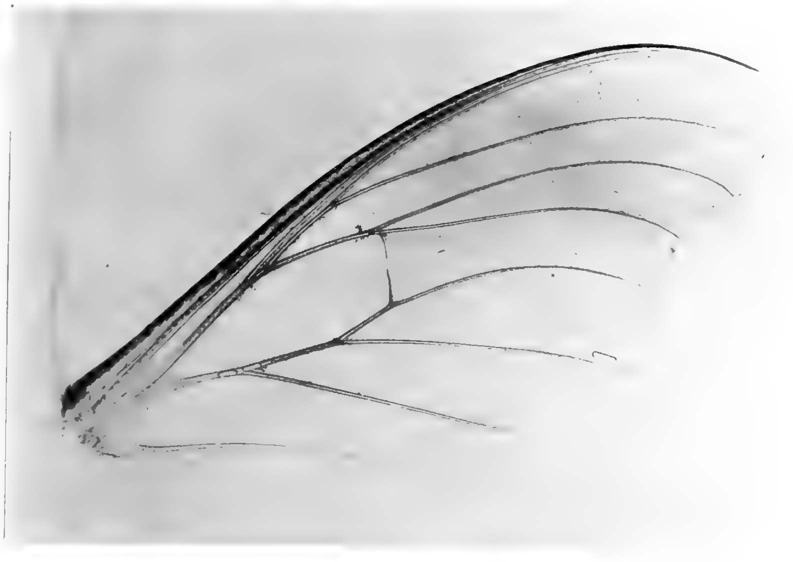


Fig. 19 Pupal hind wing of Automeris io

Fig. 20 Adult fore wing of Telea polyphemus

Plate 11

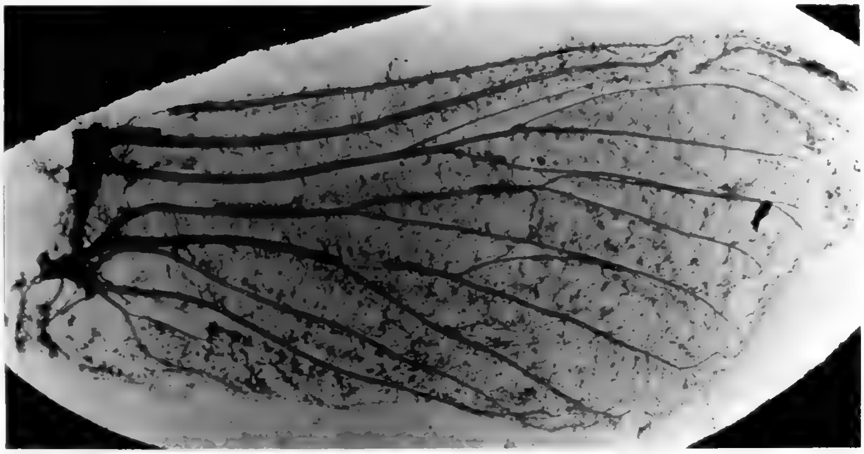
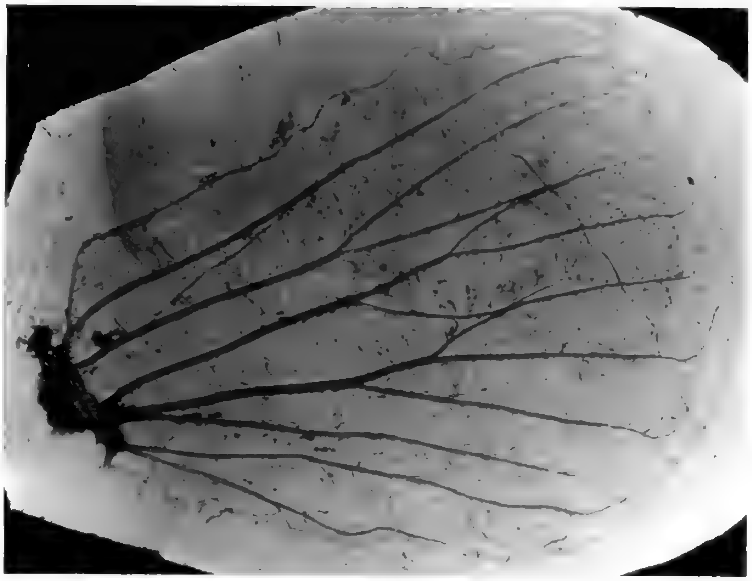


Fig. 21 Adult hind wing of Telea polyphemus

Fig. 22 Pupal fore wing of Telea polyphemus

Plate 12



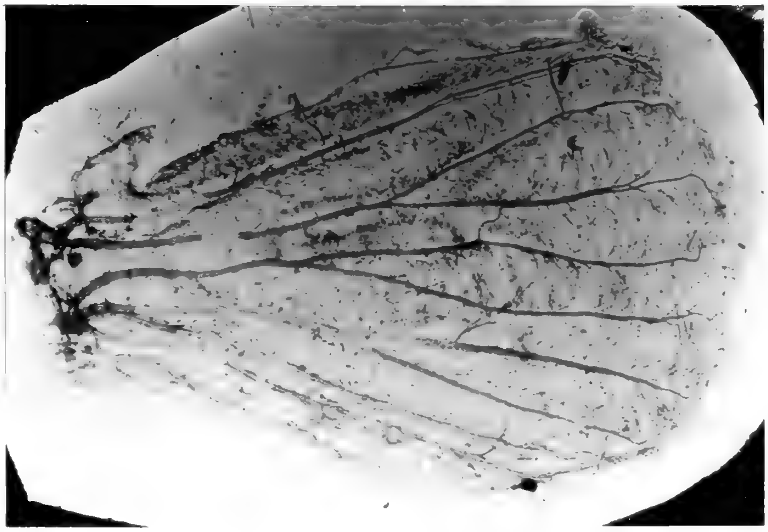


Fig. 23 Pupal hind wing of Telea polyphemus

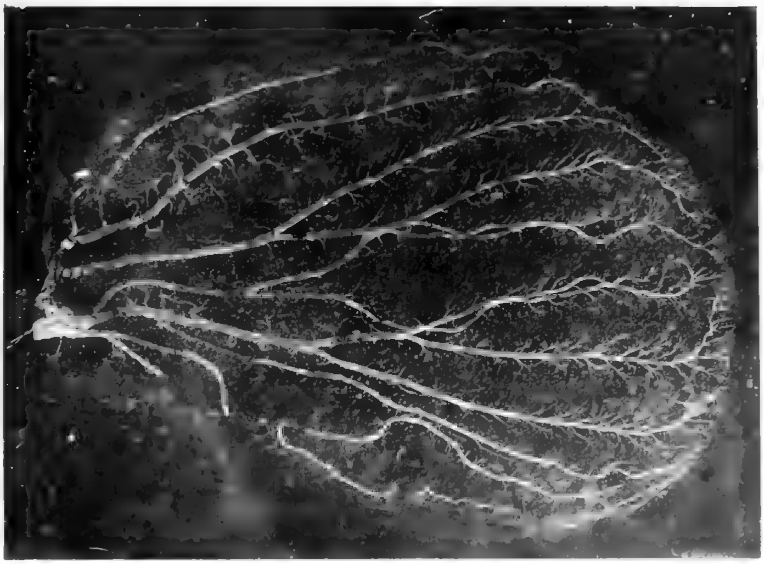
Fig. 24 Pupal hind wing of Telea polyphemus

Plate 13

Fig. 25 Adult fore wing of Callosamia angulifera

Fig. 26 Pupal fore wing of Callosamia angulifera

Plate 14



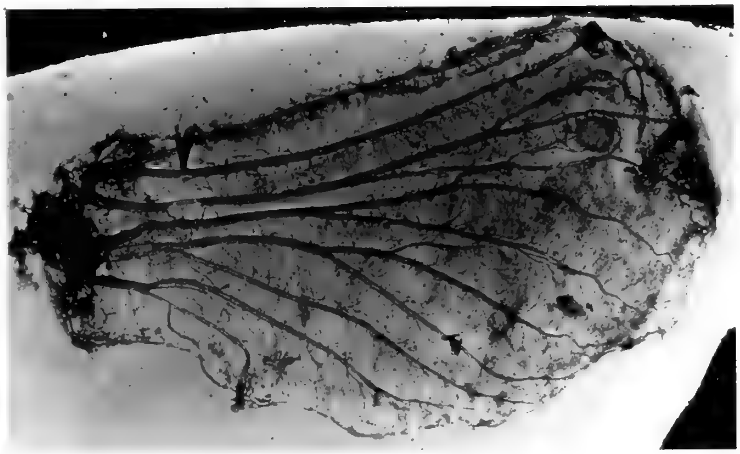
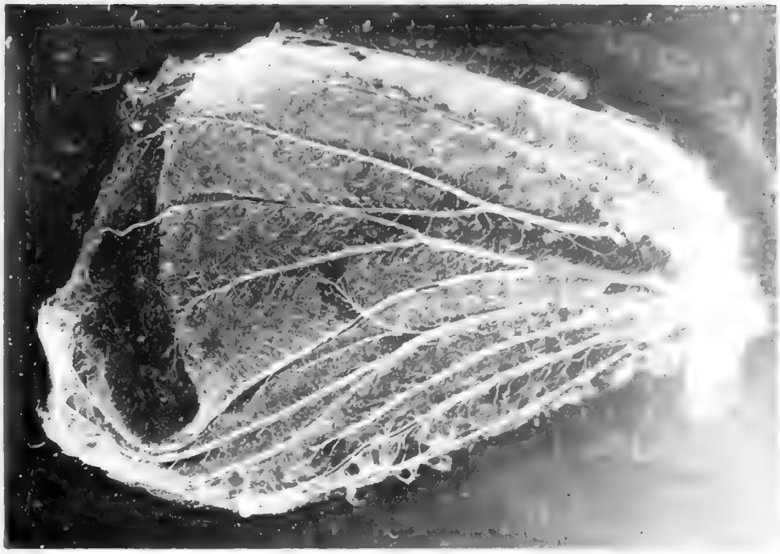


Fig. 27 Pupal hind wing of Callosamia angulifera

Fig. 28 Pupal fore wing of Tropaea luna

Plate 15



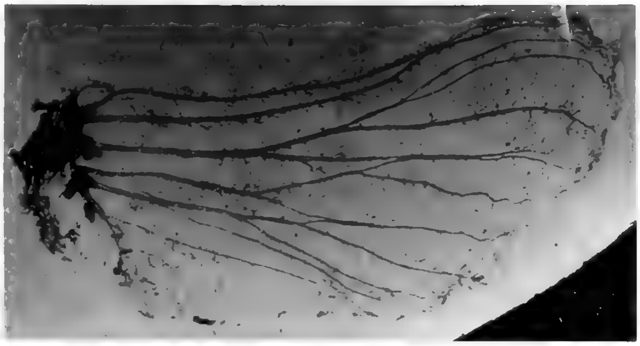
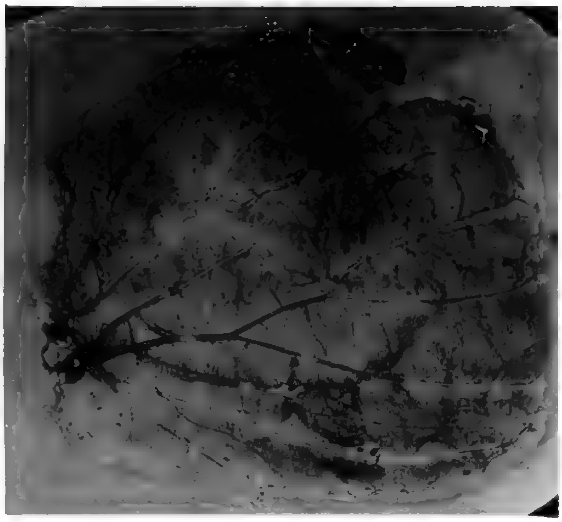


Fig. 29 Pupal hind wing of Tropaea luna

Fig. 30 Pupal fore wing of Callosamia promethia

Plate 16



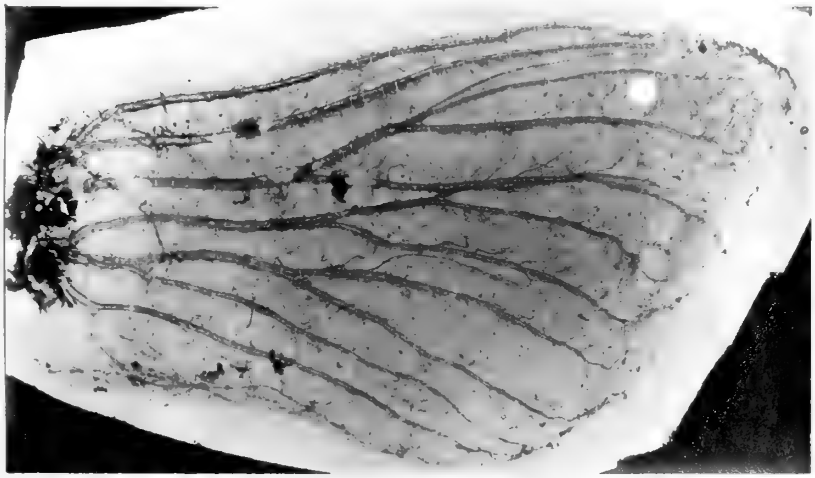
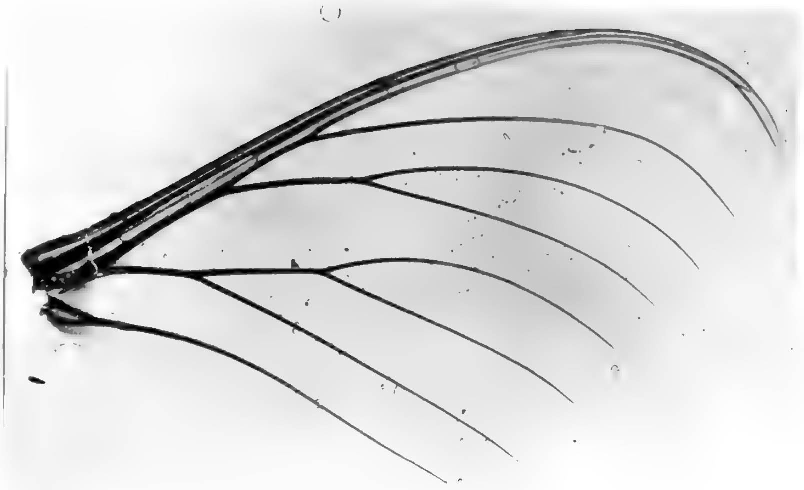


Fig. 31 Pupal hind wing of Callosamia promethia

Fig. 32 Pupal fore wing of Samia rubra

Plate 17



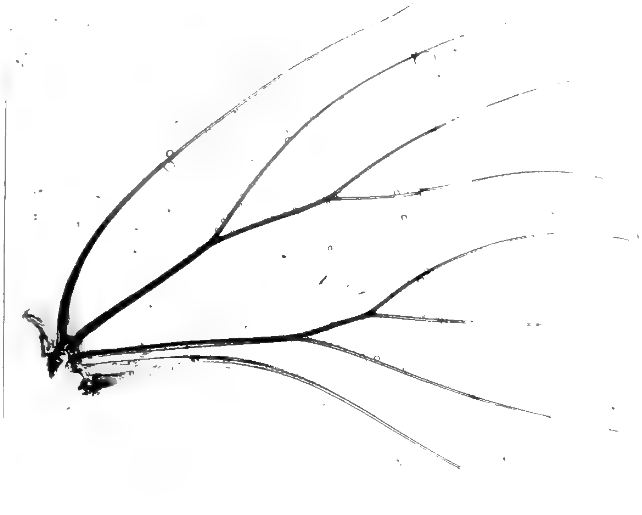


Fig. 33 Adult fore wing of Samia cecropia

Fig. 34 Adult hind wing of Samia cecropia

Plate 18

Fig. 35 Pupal fore wing of Samia cecropia

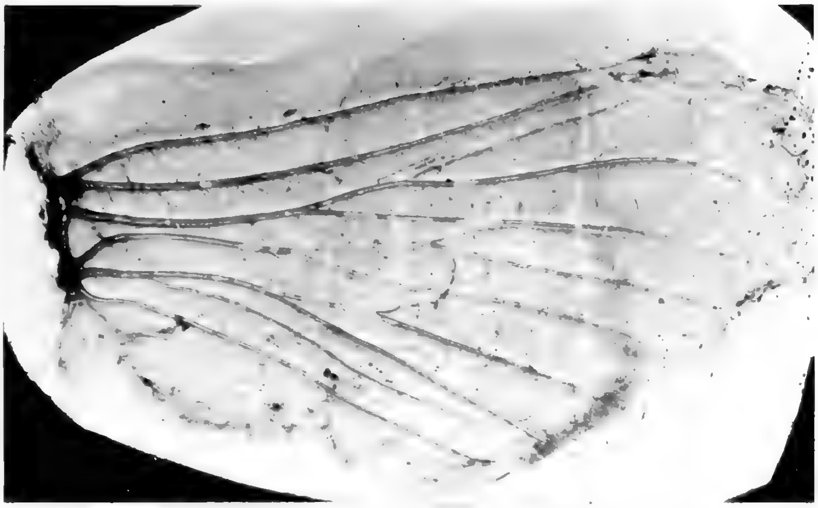
Fig. 36 Pupal fore wing of Samia cecropia

Plate 19

Fig. 37 Pupal fore wing of Samia cecropia

Fig. 38 Pupal fore wing of Samia cecropia

Plate 20



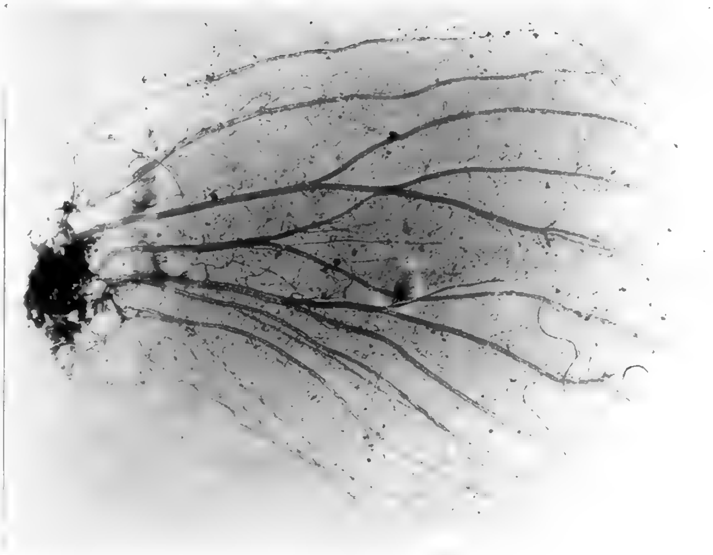


Fig. 39 Pupal fore wing of Samia cecropia

Fig. 40 Pupal hind wing of Samia cecropia

Plate 21

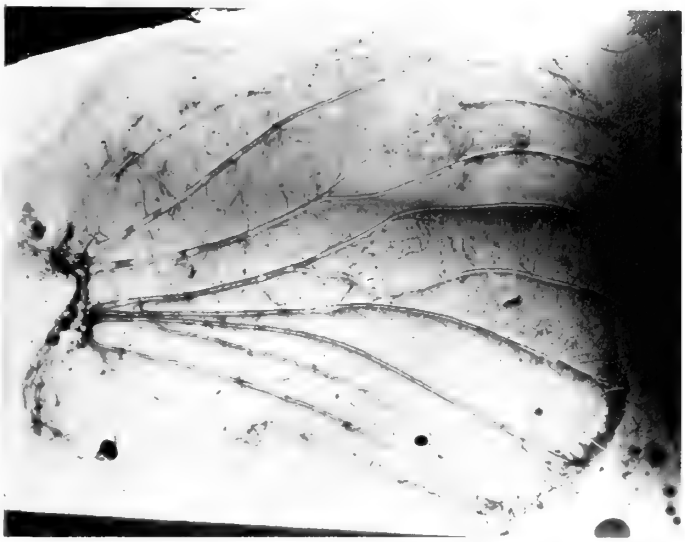


Fig. 41 Pupal hind wing of Samia cecropia

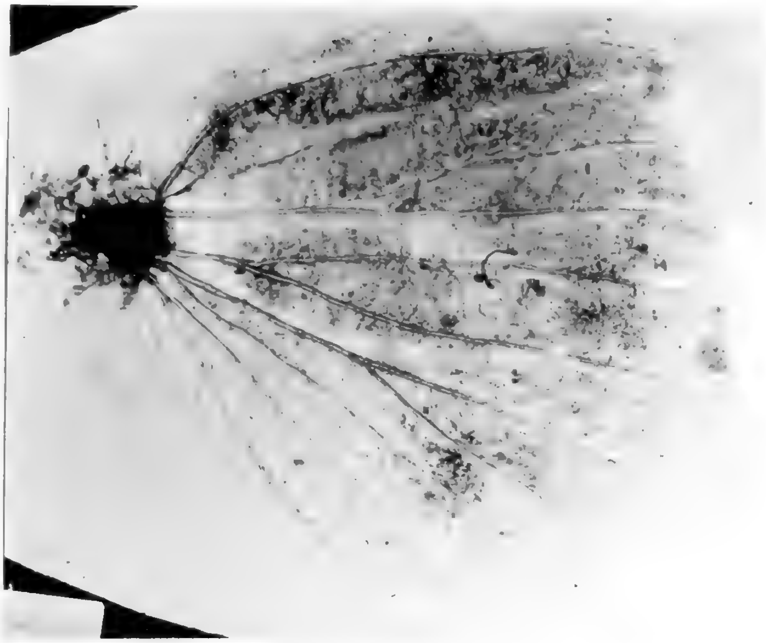
Fig. 42 Pupal hind wing of Samia cecropia

Plate 32

Fig. 43 Adult fore wing of Rothschildia orizaba

Fig. 44 Pupal fore wing of Rothschildia orizaba

Plate 23



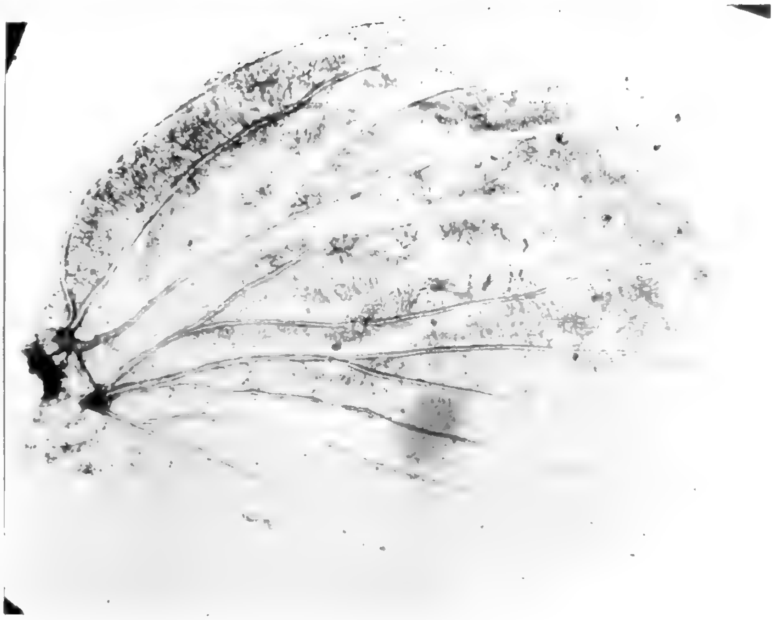
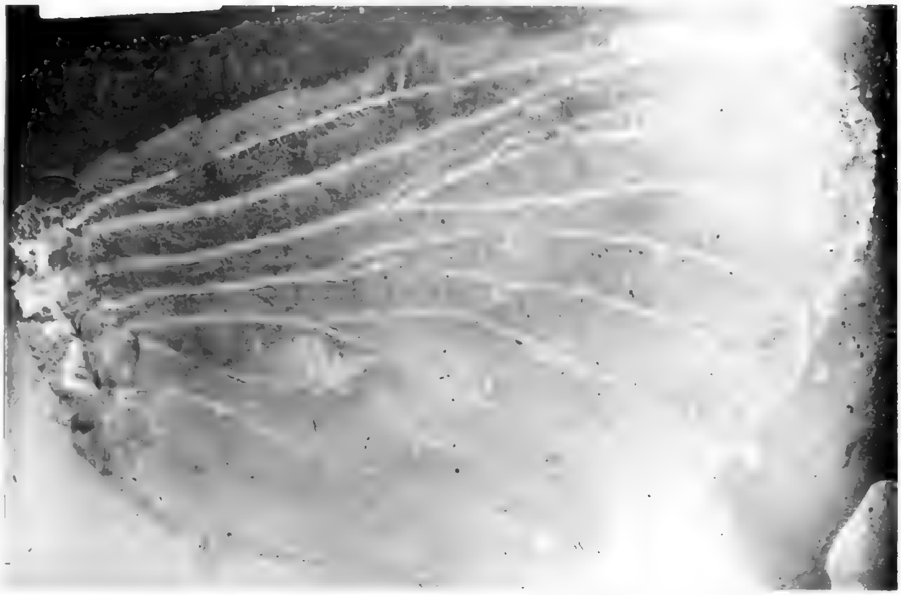


Fig. 45 Pupal hind wing of Rothschildia orizaba

Fig. 46 Pupal hind wing of Rothschildia orizaba

Plate 24



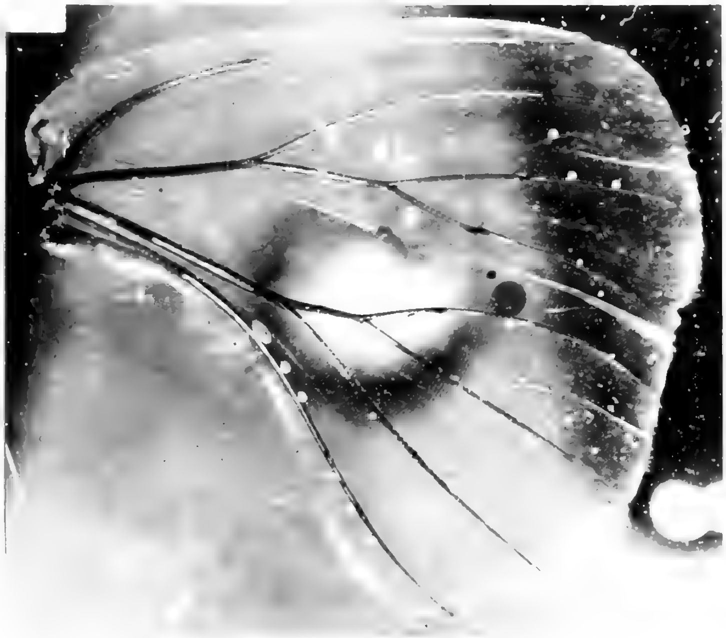


Fig. 47 Pupal fore wing of Philosamia cynthia

Fig. 48 Adult hind wing of Philosamia cynthia

Plate 25

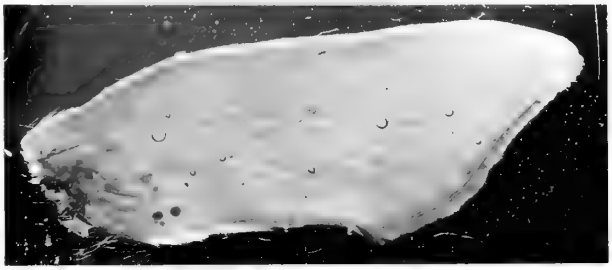


Fig. 49 Pupal hind wing of Philosamia cynthia

Fig. 50 Pupal fore wing of Ampelophaga myron

Plate 26

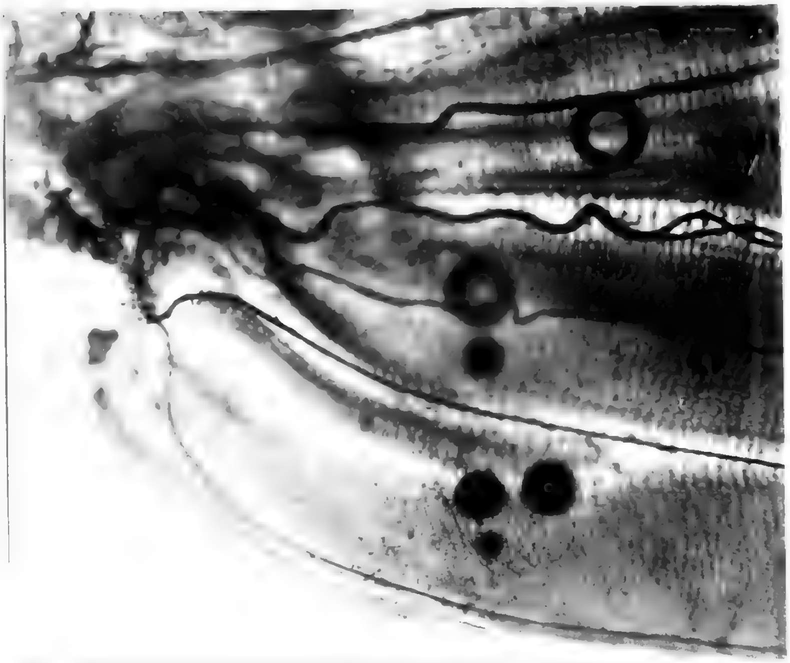
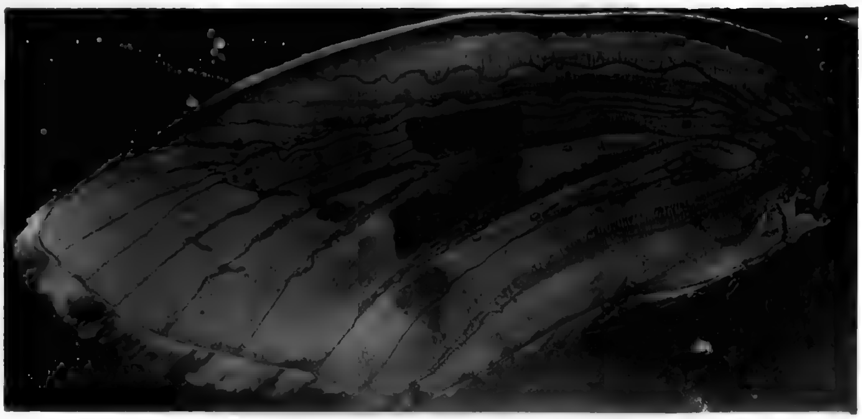


Fig. 51 Anal area of the Pupal hind wing of Amphelophaga myron

Fig. 52 Pupal hind wing of Ampelophaga myron

Plate 27



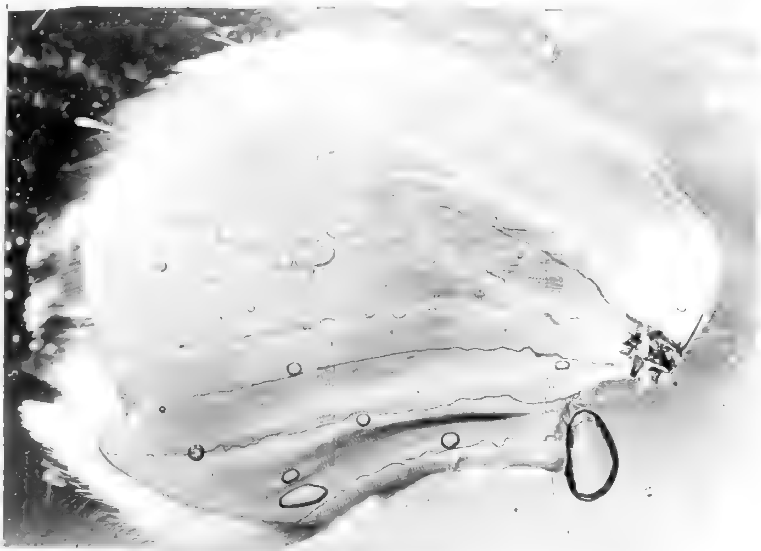


Fig. 53 Pupal fore wing of Epargyreus tityreus

Fig. 54 Pupal hind wing of Epargyreus tityreus

Plate 28

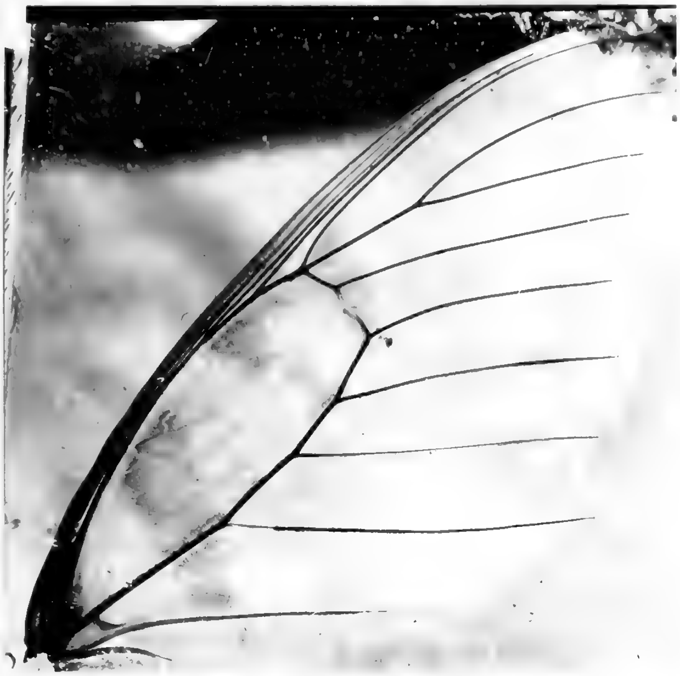


Fig. 55 Adult fore wing of Papilio turnus

Fig. 56 Adult hind wing of Papilio turnus

Plate 29

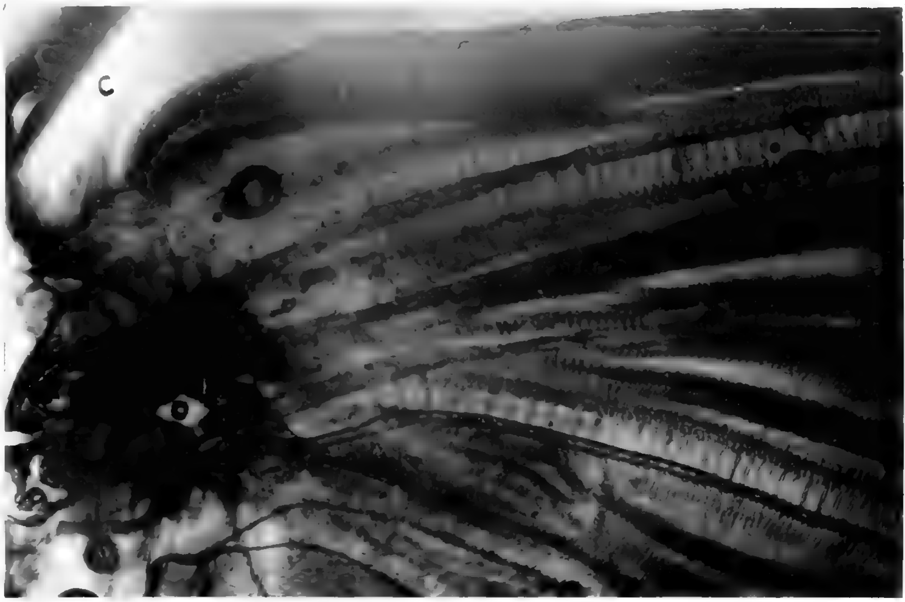
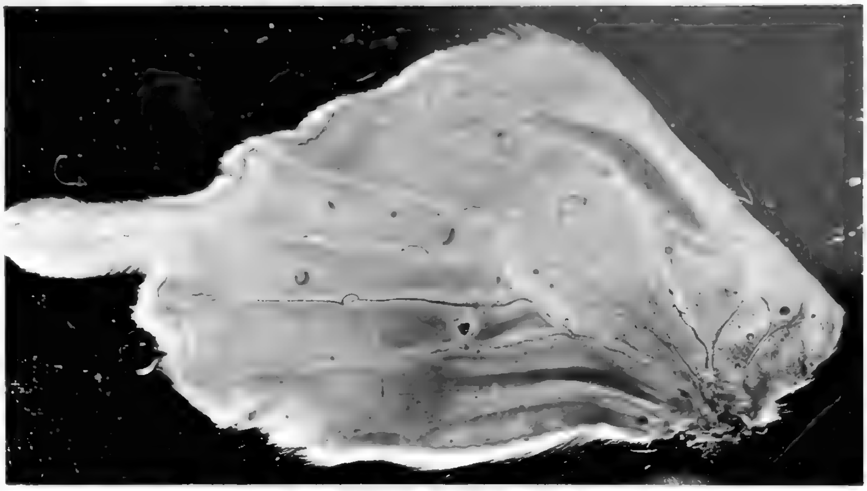


Fig. 57 Pupal fore wing of Papilio troilus

Fig. 58 Basal portion of the pupal fore wing of Papilio troilus

Plate 30



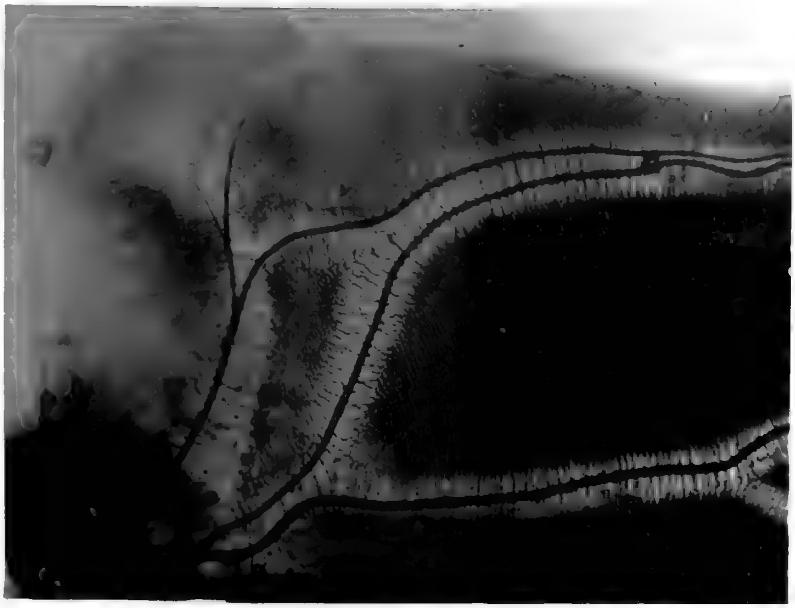


Fig. 59 Pupal hind wing of Papilio troilus

Fig. 60 Humeral area of the pupal hind wing of Papilio troilus

Plate 31

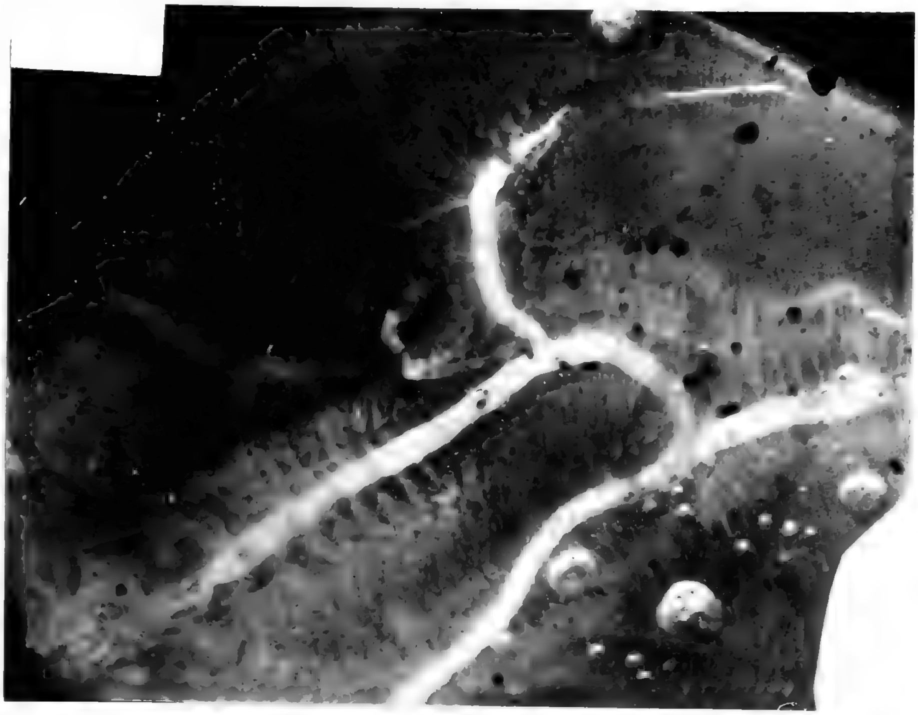
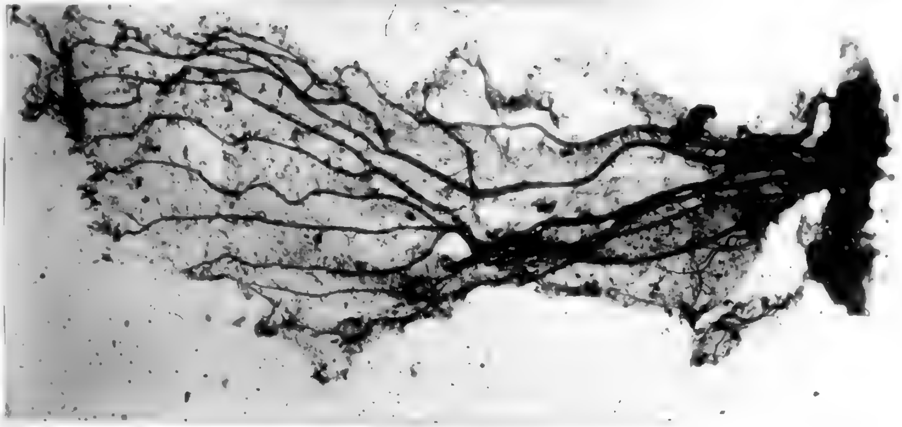


Fig. 61 Pupal hind wing of Papilio troilus

Fig. 62 Humeral area of the pupal hind wing of Papilio troilus

Plate 32



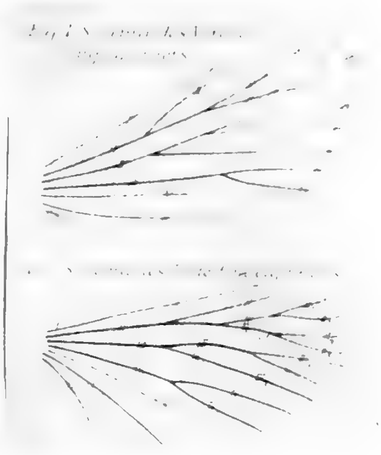
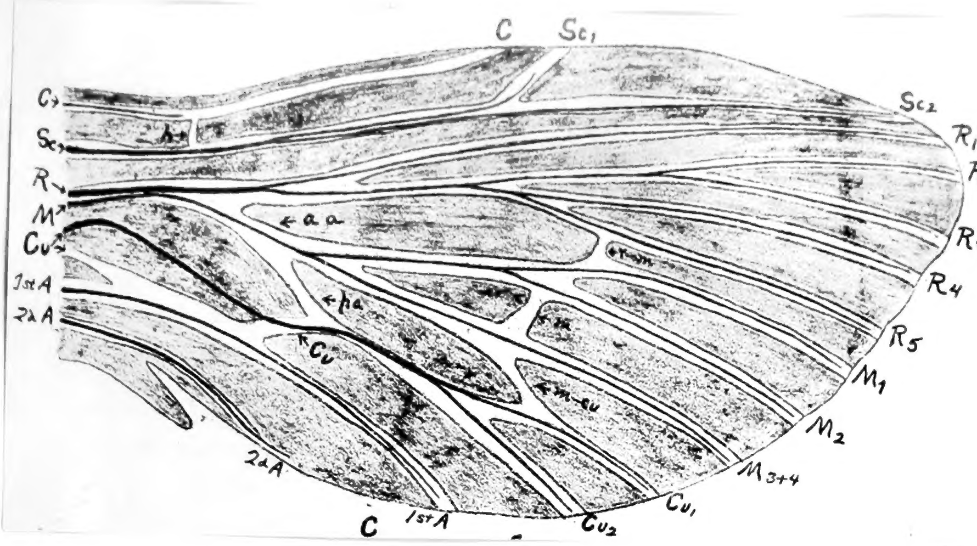


Fig. 63 Pupal fore wing of Datana ministra

Fig. 64 Spuler's scheme of the tracheation of the primitive lepidopterous wing

Plate 33



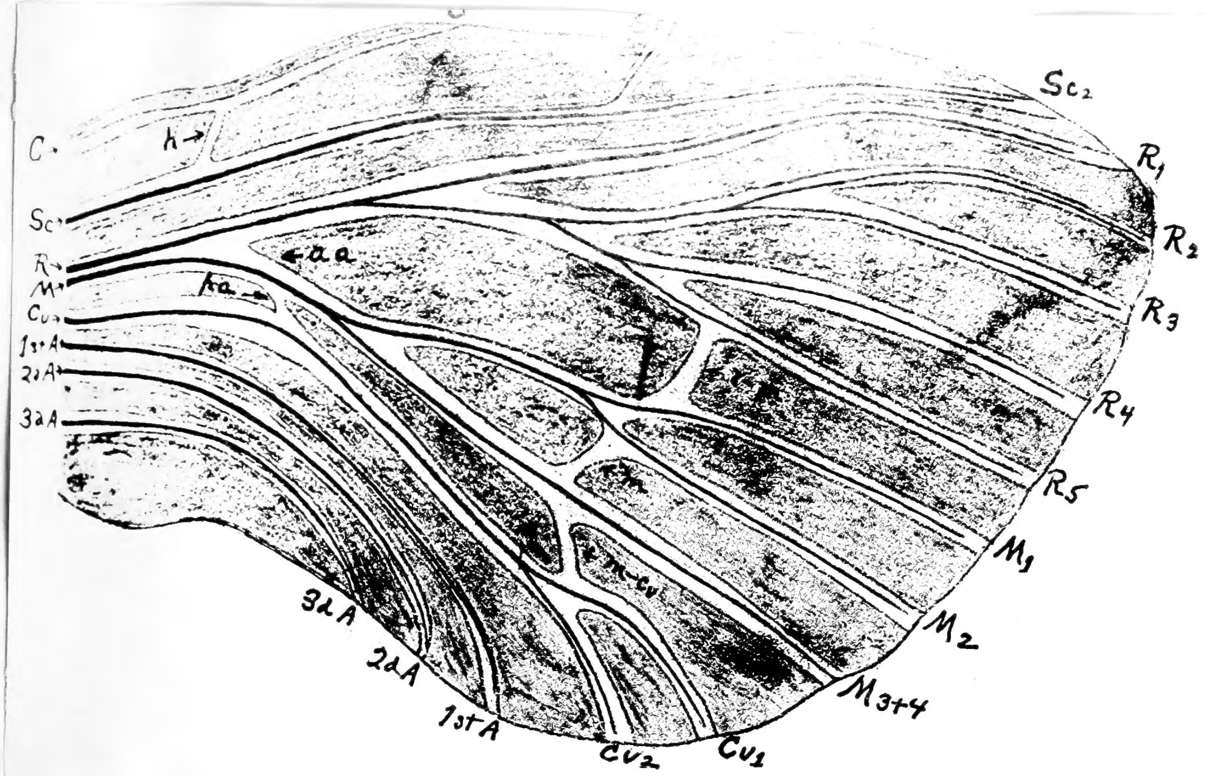


Fig. 1. Hepialus thule, pupal wings.

Figs. 65 and 66 Pupal wings of Hepialus thule, after MacGillivray