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## EVOLUTION AND TAXONOMY.

AN ESSAY ON THE APPLICATION OF THE THEORY OF NATURAL SELECTION IN THE CLASSIFICATION OF ANIMALS AND PLANTS, ILLUSTRATED BY A STUDY OF THE EVOLUTION OF THE WINGS OF INSECTS, AND BY A CONTRIBUTION TO THE CLASSIFICATION OF THE LEPIDOPTERA.

By JOHN HENRY COMSTOCK.

### PART I.

#### A PROPOSED METHOD STATED.

It is now thirty-four years since the publication of Darwin's Origin of Species ; and the great war of opinions which had been imminent for some time, and which broke forth on the appearance of that work, has been fought to a conclusion. There remains no contest except that of a healthy competition in reaping the fruits of the victory. Naturalists differ in their opinions as to details but the great principle of evolution has been firmly established, and our methods of thought have been revolutionized in consequence.

Notwithstanding this I do not believe that the systematists of to-day are making as much use of the theory of descent in taxonomic work as they might. We are still busy describing species as if they were immutable entities ; and in our descriptions we give little thought to the causes that have determined the forms of organisms. It is true that considerable has been done in the direction of working out the phylogeny of the larger groups, as branches and classes, and to a less extent of orders. But rarely is any effort made to determine the phylogeny of the smaller groups.

Here I believe lies the work of the systematist of the future. The description of a species, genus, family or order, will be considered incomplete until its phylogeny has been determined so far as is possible with the data at hand. We are to care less for the mere discovery of new forms, and more for an under-

standing of the processes by which new forms have arisen. The object of taxonomy will not be a mere grouping of forms according to similarity of structure. But the systematist will have constantly before him the question : What do these variations of form mean ? With this change in the object of taxonomic work, there will come a change in its methods. It is strange that the change has been so long delayed ; for we are really using the same methods that were employed before the establishment of the truth of the theory of natural selection. What these methods are was indicated by Darwin in the following words :

“ Practically, when naturalists are at work, they do not trouble themselves about the physiological value of the characters which they use in defining a group or in allocating any particular species. If they find a character nearly uniform, and common to a great number of forms, and not common to others, they use it as one of high value ; if common to some lesser number, they use it as of subordinate value.” (Darwin, *Origin of Species*, pp. 367-368, Am. Edition.)

This statement is about as true to-day as when Darwin wrote it. For if one will look through the taxonomic works on zoology or botany he will very seldom find any reference to the functions of organs. But almost all naturalists now believe that in each epoch of time the forms of existing organisms have been determined by a survival in preceding generations of those individuals whose parts were best fitted to perform their functions.

Does it not follow from this belief that we can confidently expect to gain much help in our efforts to work out the phylogeny of organisms by making a careful study of the functions of their organs, and endeavoring to understand the reasons for the action of natural selection ?

I suggest, therefore, that the logical way to go to work to determine the affinities of the members of a group of organisms is first to endeavor to ascertain the structure of the primitive members of this group ; and then endeavor to learn in what ways these primitive forms have been modified by natural selection, keeping in mind that in each generation those

forms have survived whose parts were best fitted to perform their functions.

Obviously there are certain difficulties in the carrying out of this plan. But the measure of our success in determining the affinities of the organisms studied, will depend largely on our ability to overcome these difficulties.

Among the difficulties encountered is the fact that usually our classification must be based largely on a study of living forms; for in most cases the aid to be derived from Palaeontology is comparatively slight. But although the record presented by fossils is very fragmentary, fortunately there are many living forms which are comparatively slightly specialized. And these will serve to give an idea of the stem form of the group.

Thus to carry out the plan suggested, the zoologist or botanist, if he is forced to work only with living animals or plants, will select from the group to be studied the most generalized type before him, and then trace out the different ways in which this type has been modified in the more specialized forms.

If the group studied be a large one, the probabilities are that instead of a single primitive type, several generalized forms will be found, each representing more or less approximately the stem form of a distinct line of development; and a comparative study of these different forms will be necessary in order to obtain an idea of the structure of their common ancestor.

But how shall one go to work to select from a large number of forms those that are to be considered the more generalized? The higher animals and plants are such complex organisms that it is not an easy matter to determine the relative degree of specialization of two distinct forms. The problem is also complicated by the fact that even the more generalized forms may present specializations peculiar to themselves.

Numerous examples will occur to any systematist of forms which as a whole are comparatively generalized, but which in some respects are highly specialized, being, as has been expressed by some writers, "sidewise developed." It is essen-

tial that these sidewise developments be not included in our conception of the still more primitive form.

Thus the Thysanura are regarded as the most generalized of the living Hexapoda. This would also be the case if of this order only the suborder Collembola were known to us. In such a case we might conclude from a study of the spring-tails that the primitive Hexapoda possessed a ventral sucker and a caudal spring, and that these organs had been superseded by the wings in more specialized forms. Now we know that while taken as a whole the Collembola are very generalized insects, that so far as the ventral sucker and caudal spring are concerned they do not represent the primitive type of the order, but are sidewise developed. In both the Cinura and the Collembola we find forms which are clothed with highly specialized scales, scales which rival in complexity of structure those of the Lepidoptera. Yet no one believes that the primitive Hexapoda were so clothed. This is another sidewise development. And the scales of the Lepidoptera, and of the Curculionidæ, for example, have arisen independently.

We thus see that although in our efforts to trace out the series of modifications through which a line of organisms has passed we may find forms which appear primitive, we must not expect to find among living forms an exact record of these changes. Each form studied will represent the tip of a twig which has separated from the main branch. Fortunately for our purpose we can often find some forms representing twigs that branched off very early and that have not grown very far in their special direction. In many cases too, forms are found which although highly specialized as regards some of their organs will retain a generalized condition of other organs. By a comparison of a number of such forms each representing a generalized condition of some of its organs we can get an approximate idea of the common progenitor.

But I repeat, how shall we determine which are the representatives of those short twigs that have undergone but little change, and which are the representatives of branches that have been greatly modified? The answer to this question is

a statement of the method I propose for applying the theory of natural selection to taxonomy more fully than has been done before.

As the structure of a highly organized animal or plant is too complicated to be understood in detail at once, it is suggested that the student begin with the study of a single organ possessed by the members of the group to be classified, and that his studies take the following course : First the variations in form of this organ should be observed, including palæontological evidence if possible ; then its function or functions should be determined. With this knowledge endeavor to determine what was the primitive form of the organ and the various ways in which this primitive form has been modified, keeping in mind the relation of the changes in form of the organ to its function. In other words endeavor to read the action of natural selection upon the group of organisms as it is recorded in a single organ. The data thus obtained will aid in making a *provisional* classification of the group.

When this stage has been reached another organ should be selected and its history worked out in a similar way.

The results of the two investigations should then be compared ; and where they differ there is indicated the need of renewed study. For if rightly understood the different records of the action of natural selection will not contradict each other. The investigation should be continued by the study of other organs and a correlating of the results obtained until a consistent history of the group has been worked out.

This method differs from that commonly employed in being a constant effort to determine the action of natural selection in the modification of the form of organisms in order to better adapt their parts to perform their function. Ordinarily little or no attention is devoted to the study of the functions of organs in purely taxonomic works.

If the history of a group be worked out in the manner indicated, the student will feel the need of recording his results in such a way as to indicate the phylogeny of the divisions of the group. But as the necessities of book making require a linear arrangement of descriptions this is somewhat difficult ; for the

natural sequence of groups should be represented by constantly branching lines rather than by a single straight line.

It seems to me that the most practicable way of meeting this difficulty is to begin with the description of the most generalized form known, and to follow this with descriptions of forms representing a single line of development, passing successively to more and more specialized forms included in this line. When the treatment of one line of development has been completed take up another line beginning with the most generalized member of that line and clearly indicating in the text that a new start has been made.

Much aid can also be given by a tabular statement of the essential characters of the subordinate groups, using the form of the ordinary analytical table. An illustration of this is given in Part III of this essay.

In this connection reference should be made to the proper position of degraded forms in a series where an effort is made to represent the natural sequence. The common practice of assigning such forms the same position that would be assigned to them if their simplicity of structure was the result of a primitive condition seems to me illogical. An example will make this point clear. The Hemiptera are doubtless all descended from a common winged ancestor. The lice, although more simple in structure than most other members of the order, do not represent the form of this ancestor as closely as do the winged members of this order. They should not, therefore, be placed first in the hemipterous series as is commonly done. It would represent the facts of nature better to place them last, as forms departing more widely from the primitive type of the order than do the winged forms. But it should be clearly indicated that although they represent the tip of one of the lines of development that line is a downward bending line.

In attempting to work out the phylogeny of a group of organisms, there will arise, I believe, the necessity of distinguishing between two kinds of characters: first, characters indicating differences in *kind* of specialization; and second, characters indicating differences in *degree of specialization of*

*the same kind.* The former will indicate dichotomous divisions of lines of descent ; the latter will merely indicate degrees of divergence from a primitive type. Thus, to draw an illustration from the following pages, it is shown that there are two distinct ways of uniting the two wings of each side in the Lepidoptera ; they may be united by a frenulum (Fig. 22) or they may be united by a jugum (Fig. 27). These are differences in *kind* of specialization, and indicate two distinct lines of descent or a dichotomous division of the order. Among those Lepidoptera in which the wings are united by a frenulum great differences occur in the degree to which this organ or a substitute for it is developed ; such differences may merely indicate the degree of divergence from a primitive type and may need to be correlated with other characters to indicate dichotomous divisions.

It is impracticable to indicate degrees of divergence from the primitive type based on the nature of the frenulum at this stage of the discussion ; but another character will serve our purpose well. In the more generalized Lepidoptera the anal areas of one or of both pairs of wings are furnished with three anal veins ; while in more specialized forms the number may be reduced to two or even to one. But the distinctions indicated by the presence of three, two, and one anal veins in different moths, are merely differences in degree of specialization by reduction of an anal area, and taken alone will not indicate dichotomous divisions. Thus if we group together all the moths that have retained three anal veins in the hind wings, such a group will contain, not merely the Microlepidoptera, as is commonly stated, but also the more generalized members of several distinct divisions of the Macrolepidoptera.

The fact is, the primitive Lepidoptera evidently possessed at least three anal veins in the hind wings (we will omit the fore wings from the discussion for the time being). In several distinct lines of development within this order the direction of specialization of the anal area of the hind wings has been towards the reduction of the number of veins in this area ; but the extent to which this reduction has gone merely indicates the degree of divergence from the primitive type. And so far



as this single character is concerned a similar degree of divergence in a similar direction may be possessed by members of widely separated divisions of the order.

But we are not entirely dependent on differences in kind of specialization for indications of dichotomous divisions. Such divisions may be indicated by differences in the order in which specializations take place.

This also can be illustrated by a study of the anal areas of the wings. It is evident that in the primitive *Lepidoptera* the fore wings as well as the hind wings possessed three anal veins. And in certain divisions of the order the direction of specialization of the anal area of the fore wings has also been towards a reduction in the number of veins. It will be shown in the concluding part of this essay that in certain divisions of the order the reduction of the anal area of the hind wings has preceded the reduction of the anal area of the fore wings; while in other divisions of the order the reverse is the case. Here is an indication of a dichotomous division. Take for example two families of moths, one of which is characterized by the presence of two anal veins in the fore wings and three anal veins in the hind wings; and the other, by three anal veins in the fore wings, and two in the hind wings. In the former, the specialization by reduction of the anal areas has begun in the fore wings; in the latter, this specialization has begun in the hind wings. And it is evident that the common progenitor of the two families had three anal veins in both fore and hind wings, and that the difference in the order in which the reduction of the anal areas has begun indicates a dichotomous division.

There will also arise, I believe, in a work of this kind a necessity for distinguishing between the essential characters of a group and those characters which are used by the systematist merely to enable students to recognize members of the group. For it seems to me that the essential characters of a group of organisms do not lie necessarily in the presence or absence of any structure or structures, or in the form of any part or parts of the body of the living members of the group; but rather in the characteristic structure of the progenitor of

the group, and in the direction of specialization of the descendants of this progenitor.

Thus, to use again the illustration given above, the Jugatæ are essentially characterized as the descendants of those ancient Lepidoptera in which the wings of each side were united by a jugum; and they are also characterized by a tendency towards an equal reduction of the veins of the two pairs of wings. While the Frenatæ are essentially characterized as the descendants of those ancient Lepidoptera in which the wings of each side were united by a frenulum; and they are also characterized by a tendency towards a greater reduction of the veins of the hind wings than of the fore wings, or, in other words, by a tendency towards a cephalization of the powers of flight. The fact that in many of the Frenatæ the frenulum has been lost, does not invalidate in the least the truth of this characterization. The loss of the frenulum, however, in certain Frenatæ renders necessary the use of some other character or characters by the systematists as recognition characters.

The recognition characters are those usually first observed by the investigator, and are those commonly given in taxonomic works. In many cases these recognition characters are also essential characters, especially in the case of groups that have been thoroughly studied. But by the taxonomic methods now commonly used search is chiefly made for recognition characters. The more skilled the systematist the more likely is he to discover and use as recognition characters those that are really essential, although the distinction pointed out here may not be recognized by him.

In the case of those groups where but few or no generalized forms have persisted till this time, the essential characters must to a greater or less extent be inferred. This is especially true of those characters which refer to the structure of the progenitor of the group. But the direction of specialization may be shown by a single representative of the group, if it be highly specialized, and we have a clear idea of the essential characters of a larger group including the one under investigation.

It must be borne in mind, however, that the direction of

specialization may undergo marked changes in the course of the history of a single line of development. Thus I feel sure that in the ancient *Frenatæ* the tendency of specialization was towards more rapid flight which tendency resulted in the preservation of the narrower winged forms. But while this tendency has been continued in certain divisions of the group to the present time, so that in these divisions the most highly specialized forms have the narrowest wings (*Sphingidæ*, *Zygæniina*), there are other divisions in which the tendency has been changed towards a different mode of flight, and has resulted in the preservation of the wider winged forms, and in these divisions the most highly specialized forms are those having the widest wings. (*Saturniina*.)

In recording the results of specialization one is apt to speak as if there were an intelligent directing force which determines the direction of specialization; or as if individuals deliberately chose the way in which they should vary from their progenitors. The fact that we are often able to arrange the members of a group in well defined series, each series culminating in a specialized form towards which the other forms approximate in varying degrees of closeness, leads to the unconscious use of such expressions. It is difficult to keep constantly in mind the extent of the thinning out process that takes place in nature, that the objects of our studies are merely a few fortunate individuals that have withstood tests that have proved fatal to the great majority. Innumerable unfortunate variations perish and leave no record; we see the fortunate ones alone; and the impression is apt to be that there is a definite progression on the part of all. Perhaps the facts of the case can be expressed as follows: The conditions which surround an organism combined with the existing structure of that organism render variations in its offspring in certain definite directions fortunate, while variations in other directions are unfortunate. As the fortunate variations alone are preserved to us the record seems to indicate a strong tendency to vary in definite directions.

In this paper the terms generalized and specialized are used in preference to low and high, which are often loosely used as

synonyms of these terms. It should be remembered that lowness or simplicity of structure may be the result of degradation, and hence does not necessarily indicate a primitive or generalized condition. The lice are the lowest of the Hemiptera; but they are by no means the most generalized of the living members of that order.

Professor Hyatt has pointed out\* that specialization may take place in two different ways: first, by an addition or complication of parts, *specialization by addition*; second, by a reduction in the number or in the complexity of parts, *specialization by reduction*. These expressions are very convenient in indicating the direction of specialization of an organ or set of organs.

Another important principle, first pointed out, I believe by Meyrick† is that "When an organ has wholly disappeared in a genus, other genera which originate as offshoots from this genus cannot regain the organ, although they might develop a substitute for it."

The truth of *Meyrick's law*, as this last principle may be termed is obvious when we consider that if a part be wholly lost there is nothing for natural selection to act upon in order to reproduce it. And even if a necessity for the organ should again arise and a substitute be developed for it, it is not at all probable that the substitute would resemble the organ so closely as to be mistaken for it.

In the application of Meyrick's law care must be taken that comparison be made only between allied forms, *i. e.*, within what may be termed a single line of descent. I recognize the fact that these expressions are indefinite, but I believe no systematist will have doubt as to my meaning.

Let me state the matter in another way. The loss of an organ is a character that merely indicates a degree of divergence from a primitive type. And so far as any single organ is concerned this stage may be reached in one line of descent very much earlier than in another. In fact the loss of an organ may be correlated in one line of descent with a very

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\* *Insecta*, page 51.

† *Trans. Lond. Ent. Soc.* 1884, page 277.

generalized condition of other characters ; while in another line of descent very highly specialized forms may still possess the organ in question.

A good illustration of this is presented by the condition of the mouth in the *Macrolepidoptera*. In many moths the mouth parts are wanting, while in other moths and in butterflies the maxillae are very highly specialized. It cannot be concluded from this fact that the mouthless forms are farther removed from the primitive type than are the sphinges and butterflies for example. A study of other structures would not support such a conclusion. We have to do in a case of this kind either with very distinct lines of descent or with a sidewise development.

In the case of the organ selected, the mouth, there comes into play, I believe, a very peculiar principle. For a long time I was greatly puzzled by the many instances in which absence of mouth parts is correlated with a very generalized condition of other structures. The explanation of this phenomenon I now believe to be as follows : Under certain conditions natural selection may tend to change the length of the adult stage. In some cases those individuals that most quickly provide for the perpetuation of the species are the ones that are most likely to have offspring. Under such conditions there would be a shortening of the duration of the adult stage until a point was reached at which it would not be necessary for the insect to take food during the adult stage, and the mouth parts would be lost in this stage.

But this shortening of the duration of the adult stage would also tend to a great degree to remove the species that had acquired it from the struggle for existence in this stage. A species that found it necessary to fly only a few hours or even days in order to provide for the perpetuation of its kind would not offer such an opportunity for the action of natural selection upon the structure of its wings and other organs peculiar to the adult, as would surely occur in a species having a longer period of flight.

## PART II.

## THE EVOLUTION OF THE WINGS OF INSECTS.

This essay is an outgrowth of an effort to determine the phylogeny of the families of the Lepidoptera, in order to decide upon a classification to be used in a general text book of Entomology. More than three years were devoted to the problem before a systematic method of procedure was adopted. This time was largely spent in a comparative study of published classifications and in an effort to determine which of these represented most accurately the facts of nature. A large part of the work yielded poor returns for the labor expended ; for it was carried on with no definite plan ; it was a blind groping in the dark.

Suddenly one day a flood of light was thrown upon the work by the recognition of the fact that a moth which I was studying (*Hepialis*, Plate I, Fig. 2) was a generalized type. I found that a knowledge of the structure of this insect gave a clue to the probable structure of the primitive Lepidoptera. And that with this knowledge it was not too much to expect to be able to trace out the various lines of descent represented by existing forms. Then began a systematic study which has resulted in the development of the method outlined in Part I of this essay.

I regret that I have been unable to apply the method as fully as I should like to before publishing it. But the results which I have been able to obtain by it lead me to hope that the publication is not premature. And as the leisure which a teacher can get for study is limited, I could not hope to make a complete application of it, even to the families of a single order, for many years.

A complete application of the method to the Lepidoptera alone will involve a study of the segments of the body as a whole, the peculiarities of development of particular segments, the structure of internal organs, the structure of organs of special sense, the various appendages of the body as antennae, mouth-parts, legs, wings, and the external appendages of the reproductive organs, the clothing of the body, in a word the

study of every structure that has been developed in these insects.

But although this extended study will be necessary before we can consider our work complete, a provisional classification can be based on the study of a single organ or set of organs. We have only to remember that such a classification is merely provisional, and that the results obtained in this way should be confirmed or corrected by the study of other organs.

Following the method indicated, the wings were selected as the first organs to be studied. These organs were chosen as the most available ones, owing to their size, and the ease with which variations in their structure could be observed. The record of the action of natural selection is recorded upon them as upon a broad page. For a long time my attention was confined to the wings of the Lepidoptera. But later I found it necessary to greatly extend my studies in order to determine the primitive type of the wings of insects. It was also necessary to study the wings of insects of other groups in order to select a nomenclature of the wing veins that would apply to all orders of insects.

Although there are great differences in the venation of the wings of insects of different orders, a study of the more generalized members of the several orders of winged insects show that the type of venation is the same for them all. This indicates two points of great scientific interest : first, wings have originated but once in the class Hexapoda, or, to state the same thing in other words, all of the orders of winged insects have descended from a common stock ; second, if all the various forms of wings are modifications of the same type, it is not too much to expect to be able to establish a uniform nomenclature for the principal elements in the frame work of the wings, *i. e.*, the principal veins, although doubtless it will be necessary to use special names in many cases for structures that have been developed secondarily.

The importance of the wings of insects for taxonomic purposes was early recognized by entomologists, as is well shown by the fact that the names of the Linnean orders are all drawn from the nature of the wings, except one, *Aptera*, and that from the absence of wings.

Although, doubtless, the great extent to which the wings are still used in taxonomy is partially due to the ease with which wing characters can be observed, still the following considerations show that such use is warranted by the facts of nature.

The chief end of existence of an adult insect is to provide for the perpetuation of the species. This resolves itself in the case of the male into seeking a mate; and in the case of the female after accepting a mate, into seeking a proper nidus for her eggs. In the case of certain insects special conditions necessitate a prolonged existence in the adult state in order to accomplish this end in the best manner; in such cases there may exist a necessity for seeking food; but in many families all nourishment is taken during the adolescent stages.

The necessity for seeking mates or for properly placing eggs, as well as for seeking food gives great importance to organs which increase the power of locomotion. It follows from this that when organs of flight had once been developed such organs would furnish an important field for the action of natural selection.

It has been indicated that there is good reason to believe that all winged insects have descended from a common winged ancestor. But we find that the primitive type of wing has been modified in many widely different ways. Hence a study of the various ways in which wings have been specialized can not fail to throw much light on the phylogeny of insects.

The fact that in some cases, notably those of most animal parasites, wings, becoming unnecessary and perhaps even detrimental, have been lost does not lessen the value of these organs for taxonomic purposes when they have been preserved.

It is often urged, that as the wings are merely appendages of the body, they are extremely liable to be modified in form; and that consequently we cannot hope to find in them a very permanent record. In other words, while it is generally admitted that variations in the framework of the wings may give us important clues as to the limits of the genera, we can not



hope to base conclusions upon them as to the limits of larger groups. But it does not follow, that because an organ is a superficial one, it is of little value in suggesting broad generalizations. We find that often the most superficial of structures are among those that were developed very early in the history of a large group, and have persisted almost unchanged in form, although more central structures have been greatly and variously modified. Thus the form of mere dermal appendages may present characters of very high value, as the hair of mammals and the feathers of birds; even the *Cetacea* have hair, and *Archopteryx* had feathers. As "the proof of a pudding is in the eating," so the value of a character for taxonomic purposes can be determined only by its use.

As to the origin of wings we have no knowledge. We have not even a generally accepted theory to account for the appearance of these structures. Many writers believe that they are modified tracheal gills. We find in many aquatic nymphs plate-like gills, some of which would need to be modified but little to function as organs of locomotion. This is especially true of the covering pieces forming part of the respiratory appendages of an Ephemerid nymph. These pieces not only



FIG. 1.—Covering-piece of tracheal gill of May-fly.

protect the gills beneath them; but probably also serve by their flapping to cause a current of water to pass over the gills. Fig. 1 represents the covering piece of a tracheal gill of an Ephemerid nymph collected at Ithaca. The step from such a structure to one that would aid in locomotion is not a great one.

But other writers think that the wings arose as keel-like expansions of the sides of the thorax. Such expansions would function as a parachute in a falling insect, as does the folds of skin in a flying squirrel, or would function both as a kite and a parachute in a leaping insect.

In support of the latter theory the netted-veined triangular prolongations at the sides of the prothorax of certain fossil insects (*Chorædodis* and *Lithomantis*, Fig. 2) are brought forward; and it is also said that a species of *Tingis* from Texas

shows on the prothorax, transparent projections of triangular form and a netted venation similar to that of the fore wings\*.

Whatever the origin of wings may have been, I think that this much is clear: they were developed to comparatively large size and were furnished with numerous veins before they began to function as *active* organs of flight. This large size and rich venation may have been the result of a natural selection of those forms best fitted to act as a kite or a parachute. But this type of wing is not well adapted for active flight. As soon as there arose a tendency for the wing to function in this way, there began, doubtless, the extensive series of modifications of which we have records both in the rocks and among living insects.

We know almost as little regarding the origin of the veins of the wings as we do of the wings themselves. Still we may be allowed to speculate regarding the matter. Let us suppose that the wings originated from broadly expanded organs; such organs would be furnished with tracheæ, even if they were used only as a parachute; for they would need to be supplied with air as are other parts of the body. On the modification of such organs into wings fitted for active flight, it would be important that the main trunks of the tracheæ



FIG. 2.—*Lithomantis*.

should be protected in such a way that any bending of the wing, which would compress them and thus choke off the supply of air, would be avoided. Thus any tendency of the membrane of the wing to become thickened along the lines of the tracheæ would be preserved by natural selection; and correlated with the development of this firm frame-work, there might be a thinning of the spaces between the main tracheæ, thus insuring lightness of the entire organ.

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\* Josef Rettenbacher, Vergleichende Studien über das Flügelgeäder der Insecten Ann. des k. k. naturhistorischen Hofmuseums, Wien, Bd. I. 153-232, t. IX-XX.

We are not entirely without evidence that this is the method of the formation of wing veins. It will be shown later that



FIG. 3.—*Palæoblattina douvillei*.

when the principal stem of one system of veins (media) is obliterated and the branches of this system are forced to derive their supply of air through lateral tracheæ extending to adjacent systems of veins, these lateral tracheæ become enveloped by veins resembling in every respect the principal veins. Similar evidence may be drawn from the study of the development of the

humeral veins in the *Lasiocampidæ*.

Since we are not able to determine the form and function of the organs which were modified into wings, let us endeavor to select the most generalized type of wings preserved to us. We will first see what light Palæontology throws upon this question

Comparatively little is known regarding the primitive insects. But thanks to the labors of Mr. S. H. Scudder, who has been one of the chief workers in this field, what is known has been made easily accessible.\*

Winged insects appeared very early, probably as early as any land plants; for Moberg has figured an insect (in the *Förhandlingar* of the Swedish geological society) from the upper part of the lower silurian; and Brongniart has figured and described a wing from the middle silurian sandstone of Calvados, France. (Fig. 3). But this wing instead of being primitive in form represents a rather highly specialized type, if the figure given correctly represents



FIG. 4.—*Homothetus fossilis*.

\* Zittle. *Traite de Paleontologie* t. II.

Bull. U. S. Geol. Survey No. 31.

Bull. U. S. Geol. Survey No. 69.

Fossil Insects of North America. Vol. I. Pretertiary Insects.

Index to the known Fossil Insects of the World, including Myriapods and Arachnids. Bull. U. S. Geol. Survey No. 71.

its structure. And the insect described by Moberg (*Protoci-mex siluricus*) is supposed by him to be hemipterous, an even more highly specialized type.

Of devonian insects we know several. Those which are best preserved are *Homothetus fossilis* (Fig. 4), *Xenoneura antiquorum* (Fig. 5), and *Platephemera antiqua* (Fig. 6). These differ among themselves to such an extent that we are forced to conclude without taking into account the two known silurian insects, that already at that early time there was a large and varied insect fauna, of which the more primitive forms have not been discovered.

From the carboniferous rocks much more abundant material has been obtained. But, according to the views of Mr. Scudder "there existed among these ancient forms no ordinal distinctions, such as obtain to-day, but they formed a single homogeneous group of generalized hexapods, which should be separated from later types more by the lack of those special characteristics which are the property of existing orders than by any definite peculiarity of its own."\*

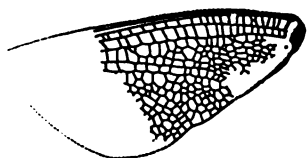


FIG. 6.—*Platephemera antiqua*.



FIG. 5.—*Xenoneura antiquorum*.

To this group of generalized hexapods which includes all paleozoic insects the name *Palæodictyoptera* has been applied.

Among the Palæodictyoptera were insects which were undoubtedly the precursors of the cockroaches, the may-flies, and the walking-sticks. Still these

groups of insects "were more closely related to one another, at least in the structure of their wings (which is the only point of general structure yet open for comparison) than any one of them is to that modern group to which it is most allied." The ordinal distinctions which is now found in the "wing structure of modern insects did not exist in

\* Bull. U. S. Geol. Survey. No. 31 p. 104.

paleozoic insects, but a common simple type of venation which barely admitted of family divisions."\*

In his classification of the Palæodictyoptera,† Mr. Scudder indicates a number of these family divisions, and groups them according to their general facies and by their relationship to succeeding types into four sections as shown by the following table.‡

PALÆODICTYOPTERA.

ORTHOPTEROIDEA.

1. Fam. *Palæoblattariæ*.  
Subf. *Mylacridæ*.  
Subf. *Blattinariæ*.
2. Fam. *Protophasmidæ*.

NEUROPTEROIDEA.

1. Fam. *Palephemeridæ*.
2. Fam. *Homothelidæ*.
3. Fam. *Palæopterina*.
4. Fam. *Xenoneuridæ*.
5. Fam. *Hemeristina*.
6. Fam. *Gerarina*.

HEMIPTEROIDEA.

*Eugereon, Fulgorina, Phthanocoris.*

COLEOPTEROIDEA.

Borings supposed to be of beetle-like insects.

It is evident from a study of the fossil remains that our knowledge of the primitive Palæodictyoptera is very fragmentary. The few forms that have been discovered in the silurian and devonian rocks are evidently more highly specialized than certain other forms which have been found in the carboniferous; the most generalized wings known to us, as I shall show later, being from this epoch. We must, therefore, turn to the carboniferous as the earliest epoch from which we have data to base our conclusions regarding the structure of the primitive insect wings.

As this is a comparatively late period we are forced to pursue practically the same method that we would were we to attempt to solve the problem by a study of living insects. That

\* Scudder. *Pretertiary Insects* p. 319, 320.

† Zittle *Traite de Paleontologie* t. II. and in *Bull. U. S. Geol. Survey* No. 31.

‡ It would be presumptuous for one who has studied the paleozoic insects so little as I have done to criticise the accepted classification of them. I therefore quote it without change, although it does seem to me that ordinal distinctions arose earlier than indicated by Mr. Scudder.

is we must select what seems to be the more generalized types and try to eliminate from these the results of sidewise developments.

What is gained by the study of carboniferous insects, I believe, is the demonstration that certain characters which have been commonly considered primitive did not exist with these insects, and consequently must be considered as secondary developments.

A comparative study of these insects show that in the Palæodictyoptera the two pairs of wings were very similar in structure both being membranous and furnished with a similar framework of veins.\* Each wing possessed six principal veins or groups of veins which are clearly homologous with the *costa*, *subcosta*, *radius*, *media*, *cubitus*, and *anal veins* of modern insects. The wings when not in use were closed over the abdomen. They were sometimes broadly folded but were never plated, as are the hind wings of the Acrididæ for example. This feature being with little doubt a comparatively late development. (See Scudder, *Pretertiary Insects*, p. 49.)

It seems to me probable that the Palephemeridæ presented an exception to the general statement given above, in that the two pairs of wings were not of equal size. The shape of the fore wings of *Platephemera antiqua* (Fig. 6) is such as to indicate that the hind wings were small. And I am informed by Mr. Scudder that the only paleozoic may-fly known that shows the hind wings at all (*Palingenia feistmanteli*) shows that they must have been broad and in all probability much shorter than the fore wings.†

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\* We find here an intermembral homology analogous to that which exists between the fore and hind limbs of Vertebrates. See an exhaustive paper by Wilder on *Intermembral Homologies*, Proc. Bost. Soc. of Nat. Hist. vol. XIV, p. 154.

†In fact I do not believe that the living May-flies are so primitive as regards their wing structure as has been commonly supposed. They have attained a high degree of cephalization of the function of flight, as shown by the reduction in size of the hind wings, and the large development of the mesothorax. The subcosta and radius are nearly parallel with the costa and closely approximated to it; the wings are well corrugated; and an extensive system of concave veins have been developed. Each of these characteristics is discussed later.

Although the wings of the Palæodictyoptera agree in the characteristics given above they present great differences of structure. How shall we decide which of the different forms is the more primitive. This I think can be done by determining the degree of their adaptation to the performance of their function.

In those insects which have the best developed powers of flight we find that the costal edge of the front wings is the strongest part of the wing, the strength being due to the presence of several strong veins which are nearly parallel. Such an arrangement is necessary to withstand the strain that is brought upon this part of the wing. I conclude, therefore, that wings possessing this structure are more highly specialized than those in which the costal edge is not strengthened in this way. Using this criterion I select that form of wing which departs most widely from this type as the most generalized form; for so important a character as this when once attained would not be lost so long as the wings were used as organs of vigorous flight. I conclude, therefore, that it is among the carboniferous coachroaches that we find the most generalized form of wing.

Owing to our limited knowledge of extinct forms, I cannot hope to present in these studies continuous series; but can only select examples which illustrate the direction or directions of specialization of particular parts, without strictly confining myself to a single line of development.

In *Mylacris anthracophilum* (Fig. 7) the wing is furnished with five sets of veins in addition to the costal or marginal vein if this exists. Three of these which occupy the intermediate area of the wing arise each in a single strong trunk. These veins may be designated beginning with the one nearest the costal margin as the *radius*, *media*, and *cubitus*, respectively.



FIG. 7.—*Mylacris anthracophilum*.

Lying between the costal edge of the wing and the radius there is a group of veins which radiate from near the base of the wing (Fig. 7, II). These I believe represent the *subcosta* in its most generalized form.

These subcostal veins resemble very closely in form and arrangement the group of veins lying behind the cubitus, the *anal veins*. In fact a longitudinal line drawn through the center of the wing divides it into two nearly similar halves.

It will be readily seen that this type of wing is poorly fitted for active flight; the costal edge lacking the strength necessary for this purpose. In fact the arrangement of the veins approximates that of the covering piece of a tracheal gill figured above (Fig. 1), or that of the lateral appendages of the prothorax of *Lithomantis* (Fig. 2).



FIG. 8.—*Necmylacriss heros*.

In *Necmylacriss heros* (Fig. 8, II) we see the beginning of a strengthening of the subcostal area. One of the subcostal veins, the hindermost, becomes the principal vein of this area; and most of the other subcostal veins have become consolidated with this one, so as to appear to be branches of it. The subcostal area is also relatively much narrower.

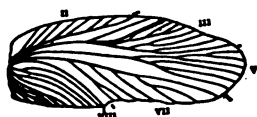


FIG. 9.—*Ectoblattina lesquereuxii*.

In *Ectoblattina lesquereuxii* (Fig. 9) the tendency of the many subcostal veins to become consolidated into a single strong vein with branches extending to the costa is carried much farther; and the narrowing of the subcostal area is also more marked.

The step from the form of the subcosta in *Ectoblattina* to that presented by many modern insects is not a great one, as for example, that of the fore wing of *Corydalis*.

It is probable that correlated with the lengthening and narrowing of the subcostal area in these paleozoic insects a thickening of the costal edge of the wing took place, thus forming the costal vein. As I have been able to study only figures of these paleozoic remains, I am unable to decide at what point in the development of the wing a distinct costal vein was formed. It was probably very early; for Mr. Scudder states that in the paleozoic insects the six principal veins



were always developed, the marginal [costa] simple and forming the costal border.

From this brief study of the development of the subcostal area let us pass to the area lying next to the opposite margin of wing, the anal area, omitting for a time any discussion of the three veins (radius, media and cubitus) which occupy the central portion of the wing.

A striking feature in the structure of the wings of many insects is the separation of the anal area from the remainder of the wing by a fold or furrow, along the bottom of which extends a vein. Such a depressed vein has been termed, on account of its position, a *concave* vein; and in contradistinction to such veins, those veins which extend along the summit of ridges, or which are more prominent on the upper surface of the wing than on the lower, are termed *convex* veins.

This furrow separating the anal area from the preanal portion of the wing appeared very early. It is especially prominent in all cockroaches both fossil and living; and can usually be recognized in any insect wing in which the anal area is well developed. I have been unable to determine the significance of it. But have found it a very useful mark in defining the limits of the anal area. It is vein VIII of the nomenclature adopted in this paper.

The primitive form of the anal area is probably well shown in *Mylacris*, (Fig. 7), where it closely resembles the primitive form of the subcostal area, as shown in the same genus. But the latter specialization of this area has been very different from that of the subcostal. This specialization has taken place in two opposite directions, *i e.*, by reduction and by addition.

In certain lines of development the tendency of natural selection has been to preserve the narrower winged forms. And the narrowing of the wings has taken place largely through a partial or complete reduction of the anal area. The dragon-flies, *Odonata*, and the ant-lions, *Myrmeleon*, are examples of the extreme result of this tendency. And in the Lepidoptera there are several instances where a good series illustrating successive stages in this reduction can be

found. Thus within a single family, or perhaps superfamily, the more generalized members have three anal veins in at least one pair of wings, (usually the hind wings), while as one passes to more and more specialized forms only two, or one anal veins are found.

I believe that this selection of the narrower winged forms is the result of the survival of those forms that are best fitted for rapid flight. A good illustration of the difference in the powers

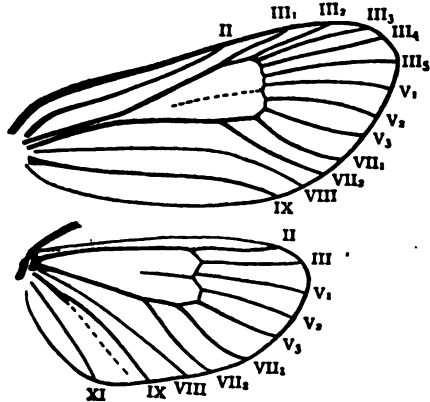


FIG. 10.—*Triprocris*.

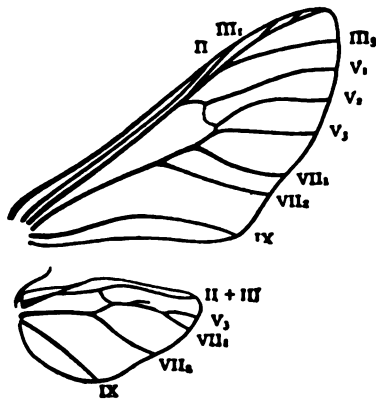


FIG. 11.—*Syntomis*.

of flight between an insect with a wide anal area and one in which this area has been reduced, can be found within the limits of a single lepidopterous superfamily, the Zygænina. Compare the power of flight of *Triprocris* (Fig. 10) in which there are two anal veins in the fore wings and three anal veins in the hind wings, with that of *Syntomis* (Fig. 11) in which there is only a single anal vein in both fore and hind wings.

On the other hand, in other lines of development, natural selection has evidently tended to a preservation of the wider winged forms; and the widening of the wings has taken place largely by a specialization of the anal area by

addition. The extreme result of this method of specialization is presented by the Orthoptera and especially by the hind wings of the Acrididæ. Here we find a widely expanded anal area, with regularly alternating concave and convex veins. Such a wing is not fitted for striking vigorous and rapid blows upon the air as is required for rapid flight; but is adapted to a sliding flight, a sliding up like a kite or down like a parachute. Such a method of flight would naturally reach its highest development in jumping insects, like the Acrididæ.

A study of the illustrations just given shows that where the tendency of natural selection is towards the development of a rapid flight there is usually a cephalization of the function of flight, *i. e.*, the hind wings are greatly reduced, and the fore wings become the chief organs of flight. This is well shown by the more specialized Zygænid (Fig. 11); and the extreme of such a cephalization is presented by the Diptera. That such a cephalization is not absolutely necessary to rapid flight is shown by the dragon-flies (Odonata); but here the abdomen is greatly elongated, which gives a similar result.

On the other hand where an expansion of an anal area has taken place in order to provide for a sliding flight, it is the hind wings that are specialized by addition, *i. e.*, the opposite of cephalization takes place. The Acrididæ have already been cited as an illustration of this.

The region lying between the subcostal and anal areas is traversed by three principal veins and their branches. These veins as already indicated, are the *radius*, *media* and *cubitus*, the radius lying next to the subcosta, the cubitus next to the anal area, and the media, between the radius and cubitus. Very remarkable modifications take place in the structure of these veins and in their relation to each other. Some of the modifications will be discussed in detail later; in this place I wish only to make some very general statements.

If a large series of wings be examined it will be found that the area of each of these veins may be specialized either by addition or by reduction, *i. e.*, it may be either widened or narrowed. When the tendency of natural selection is to widen one of these areas, the points of origin of the branches

of the principal vein will be nearer the base of the wing in the more specialized forms than in the more generalized members of the same group. On the other hand when the tendency of natural selection is to narrow one of these areas the branches become consolidated with the main stem to a greater and greater distance from the base in the more and more specialized forms. This consolidation of a branch with the main stem or of two branches with each other may extend to the margin of the wing, and thus the number of branches be reduced. This migration of the point of origin of a branch of a

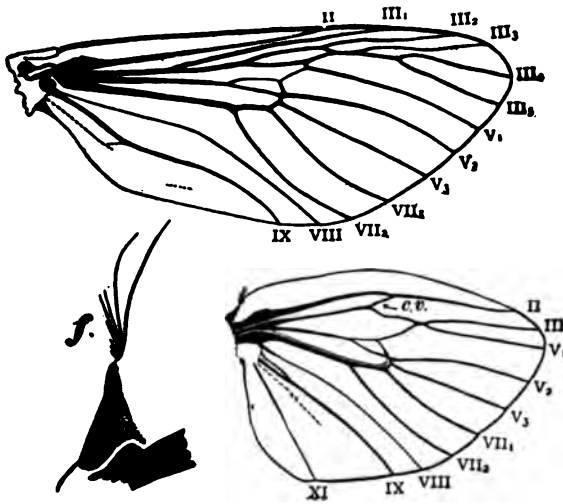


FIG. 12.—*Prionoxystus*; *f.* frenalum and frenalum brace, enlarged.

vein often affords an excellent clew to the degree of departure from a more generalized type.

But the most remarkable of the changes which take place in this region of the wing is an abortion of the main trunk of media and a consequent uniting of the branches of this vein either with cubitus or with both cubitus and radius. Excellent illustrations of this occur in the *Lepidoptera*. In many of the more generalized moths the main trunk of media is well preserved (Fig. 12); while in more specialized forms it is en-

tirely wanting. Sometimes, as in *Danais*, remnants of the basal part of the branches of media project back into the discal cell from the discal vein (Fig. 13); while in many other butterflies the branches of media are so completely united with radius and cubitus that there is no indication of the fact that they do not belong to these systems of veins (Fig. 14).

It is probable that in none of the Palæodictyoptera were the wings plaited, as they are in many existing insects; although

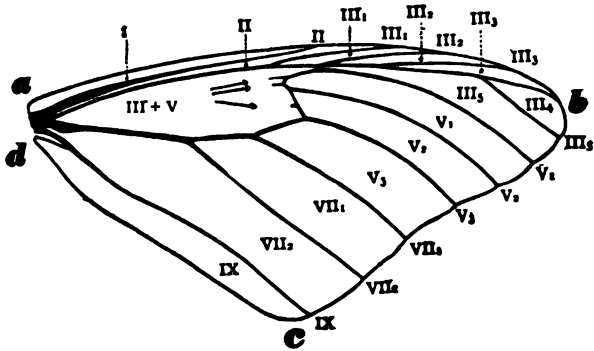


FIG. 13.—Fore wing of *Danais*.

in some, they were broadly folded. And if we except the anal furrow (vein VIII), already referred to, all of the veins were of the type that is termed convex; that is, they were more prominent on the upper surface of the wing than on the lower.

We thus see that the evidence of the Palæodictyoptera does not corroborate the theory of Adolph and Redtenbacher as to the primitive type of the wings of insects. Instead of the primitive wing consisting of regularly alternating concave and convex veins, as described by them, it is probable that the concave veins are a later development, either arising *de novo* or being modified convex veins, excepting always the anal furrow (vein VIII), regarding the origin of which we know nothing.

Concave veins have evidently arisen to meet two distinct needs: first, in those insects in which the wings have become

broadly expanded so as to provide for a sliding flight, there is a necessity for the plaiting of these wings when not in use so that they may be carried without impeding locomotion on foot ; second, we find in certain cases where the tendency of specialization has been towards a narrowing of the wings in order to admit of vigorous flight, a corrugation of the wings has taken place in order to strengthen them. The hind wings of a grasshopper illustrate the first ; and the wings of a dragon fly present the extreme of the second form of specialization.

It is easy to see that a corrugated wing, like that of the dragon fly, is much stiffer than it would be if the membrane extended in a single plane. If one will examine the cross veins extending between the costa and the radius in a dragon fly, he will find that some of these are in the form of triangular braces which effectually prevent any tendency on the part of the wing to become flattened. Evidently the corrugation is of extreme importance.

The concave veins have arisen in two ways. The first of these is by a change in the position of a convex vein. The subcosta in most of the orders of insects is an illustration of this. In the *Lepidoptera* the subcosta has retained its form as a convex vein, but in most orders of insectst he area between the costa and the radius has been depressed forming a furrow along the bottom of which the subcosta extends. This corrugation has resulted from the need of a stiffening of the costal edge of the wing. The second method of formation of

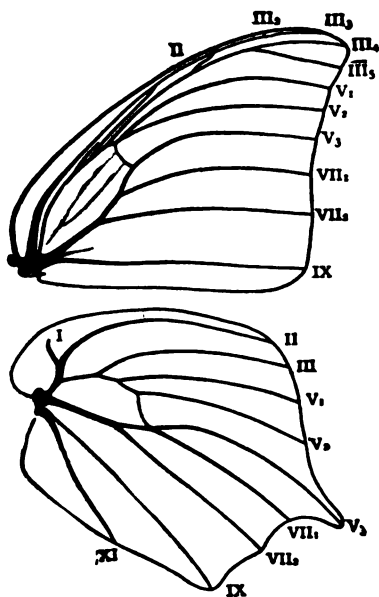


FIG. 14.—*Paphia*.

concave veins is illustrated by a vein that lies between radius and media (vein IV), and also by a vein that lies between media and cubitus (vein VI) in certain orders of insects. These veins (IV and VI) I do not believe existed in the Palæodictyoptera ; at least, I have not been able to find any indication of their presence in the figures of paleozoic insects. In the more modern orders of insects when a corrugation of the wings arose, and the areas traversed by these veins became depressed, veins IV and VI appeared. It is probable that they were developed by a straightening out of the zigzag line between two series of cells. This can be readily seen by comparing the wing of one of the devonian may-flies (Plate III, 3) with that of a modern may-fly (Plate III, 5). In the devonian may-fly the cells of the wing are polygonal, while in the modern may-fly they are quadrangular. In the latter case not only have longitudinal concave veins been formed from zigzag lines, but the cross veins extending between these concave veins and the adjacent convex veins have become strictly transverse. An arrangement which insures the preservation of the corrugations.

In a similar way the concave veins in the anal area of the modern Orthoptera have probably arisen.

I conclude, therefore, that in the more highly specialized wings of certain orders of insects, there exists a regular alternation of convex and concave veins, this alternation being the result of a corrugation of the wings for the purpose of stiffening them. This conclusion is quite different than that reached by Redtenbacher, who starts with the fan type of wing as the primitive one.

In the Lepidoptera this corrugation has not taken place, the wings being stiffened by scales, consequently, the subcosta remains a convex vein, and veins IV and VI have not been developed. It is probable that these veins are also lacking in the wings of the Hymenoptera and the Coleoptera, but I have not studied carefully the wings of these insects.

As to the nomenclature of the wing veins of insects, there is no longer any doubt regarding the desirability of a uniform system of naming the veins in the different orders of winged

insects. Only by such a system can those comparisons be made which are necessary in any thorough study of the relationship of the orders to each other. Heretofore the students of each order have had their peculiar nomenclature, and in many cases writers treating of a single family have proposed a set of names to be used in that family alone. The matter has been further complicated by the fact that not only have different names been applied to the same vein, but the same name has been applied to different veins. Thus the terms *costa* and *subcosta* have been applied by Lepidopterists to different veins than those that bear these names in other orders.

There have been several attempts to establish a uniform nomenclature. Of these that of Redtenbacher is the most important, being based on a much more extended study of the subject than that made by any other author.

Redtenbacher was the first one to work out a system and apply it to all of the orders of winged insects. And although his system was based on what I believe to be a false theory, and his interpretation of facts in some cases were faulty, I believe that the more essential features of his system can be adopted.

Although, as I have pointed out above, the fan-type of wing was not the primitive type, it seems desirable to base our nomenclature on this type; for here we find the maximum number of veins; and our nomenclature should include the secondarily developed veins of modern insects as well as the primitive veins.

I have shown that in the preanal portion of the wing of paleozoic insects there were developed five principal veins. These may be designated, beginning with the one on the costal margin of the wings, as *costa*, *subcosta*, *radius*, *media* and *cubitus*. The term *media* was proposed by Redtenbacher; the others were adopted by him as those sanctioned by the best usage.\* I have also shown that in certain insects there

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\* Redtenbacher was not the first to recognize *media* as a principal vein. This was done by Edward Doubleday nearly fifty years ago. See his Remarks on the Genus *Argynnis*, Trans. Linn. Soc. Vol. XIX, 1845. I have adopted the term *media* in preference to *discoidal vein* proposed by Doubleday as the latter might be confused with *discal vein*, the term commonly applied to certain cross veins.



is developed, secondarily, a longitudinal vein between radius and media, for this I propose the term *premedia*; and also in the same insects there is developed a longitudinal vein between media and cubitus, this I designate as *postmedia*.

Following the system of Redtenbacher these veins may also be designated by Roman numerals. The equivalence of the numbers and names of the veins of the wing is indicated by the following table; also the nature of the veins.

I.—Costa . . . . .	convex.
II.—Subcosta, usually	concave, secondarily.
III.—Radius . . . . .	convex.
IV.—Premedia . . . . .	concave.
V.—Media . . . . .	convex.
VI.—Postmedia . . . . .	concave.
VII.—Cubitus . . . . .	convex.
VIII.—First anal . . . . .	concave.
IX.—Second anal . . . . .	convex.
X.—Third anal . . . . .	concave,
<i>et al.</i>	

It will be seen from this table that if we consider subcosta a concave vein, which it has come to be in the larger number of the orders of insects, there is a regular alternation of convex and concave veins, when the maximum number of veins is present. And hence the convex veins are designated by odd numerals and the concave veins by even numerals; this is one of the chief features of Redtenbacher's system, and an exceedingly useful one.

If this system be applied to the anal area, and I believe it is best that it should be, all convex anal veins must be designated by odd numerals. In those orders where the anal area has been greatly specialized by addition, (*e. g.*, Orthoptera), this would naturally follow; for there we find a regular alternation of concave and convex veins. But in certain other cases it is not so obvious. In those Lepidoptera in which three anal veins are preserved, the first (vein VIII) is concave, and doubtless represents the primitive anal furrow; the second is convex and is obviously vein IX; but the third is also convex! Shall this be designated as vein X, or as vein XI? It seems to me better that we consider vein X absent,

as are veins IV and VI in this order, and designate this one as vein XI. This view is strengthened by the fact that in many of the Microlepidoptera with broad hind wings there is a prominent fold between the two convex anal veins. This fold may be looked upon as the beginning of an anal vein, which is as yet undeveloped, but which if developed would be vein X.

Another important feature of Redtenbacher's system is the designating of the branches of a vein by Arabic indices appended to the Roman numeral indicating this vein. Thus the branches or radius are designated as III<sub>1</sub>, III<sub>2</sub>, III<sub>3</sub>, etc., (Fig. 15).

While I believe that we are able to trace out homologies between the *principal veins* of the wings of insects of the different orders, I do not think it practicable, even if possible, which I doubt, to homologize the *branches* of the principal veins beyond the limits of a single order. I have not, therefore, adopted in all cases Redtenbacher's plan of using odd indices only for convex branches and even indices only for concave branches. This plan will be found very useful in those orders (*e. g.*, Ephemera) where the fan-type

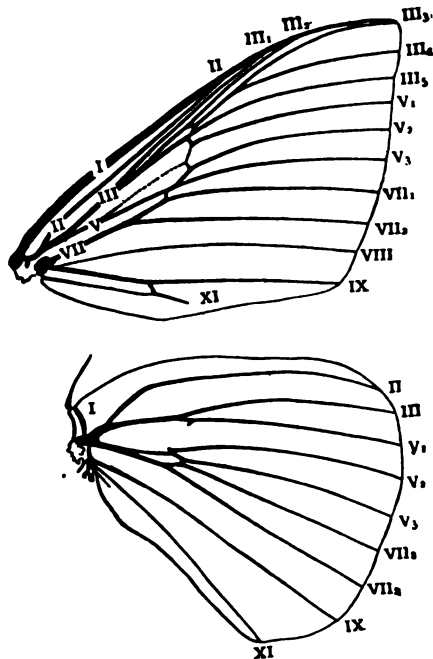


FIG. 15,—*Castnia*.

of wing has been developed ; but in other cases (*e. g.*, Lepidoptera) it would merely complicate the nomenclature without ad-

ding to its value. Thus in the Lepidoptera I designate the five branches of radius as III<sub>1</sub>, III<sub>2</sub>, III<sub>3</sub>, III<sub>4</sub>, and III<sub>5</sub>, respectively, although all of these branches are convex.

It should be noted that in numbering the branches of a principal vein, they are numbered in the order in which they reach the margin of the wing, not in the order in which they are given off from the main stem. The system adopted is not only the simpler but insures the same number being applied to homologous veins in different genera, which would not be the case were the other system adopted.

Having indicated the more general features in the development of the wings of insects in order to define the nomenclature of the wing veins that I have adopted, and having explained this nomenclature, I can now pass to the consideration of certain details exhibited by the wings of the Lepidoptera.

The more important of these are the changes which take place in *media*; for this vein in the Lepidoptera is of the highest value for taxonomic purposes.

The tendency to abortion of the main trunk of *media* has already been pointed out. The explanation of this tendency I have not fully determined satisfactorily to myself, I can only suggest the following: In the course of the narrowing of the wing and the strengthening of the main veins which has taken place as a result of a natural selection of the more active flying forms, the veins have become crowded together at the base of the wing. The more important veins, *i. e.*, radius and cubitus, have held their place, while *media* has been crowded out. This crowding out has probably taken place in this way. The narrowing of the space occupied by *media* compressed the large trachea or tracheæ which it contained. Such a compression tends to shut off the supply of air to that part of the wing supplied by the branches of *media*. To counteract this evil, communication is established between the branch of *media* and the veins lying on either side of it. When such a communication is well established there is no longer any need for the basal portion of *media* and it becomes atrophied. In this connection it should be stated that the mem-

brane of the wing is supplied with an immense number of minute tracheæ extending from the main trunks contained in the veins. The lateral branches of the tracheæ are rarely seen even in carefully bleached wings, for in mounting the specimen they become filled with the mounting medium and are thus rendered invisible. But occasionally air will remain in them rendering them distinctly visibly. It is by means of some of these lateral tracheæ that the branches of media become connected with radius and with cubitus.

When such a communication has been established it is important that these tracheæ should not be compressed by the

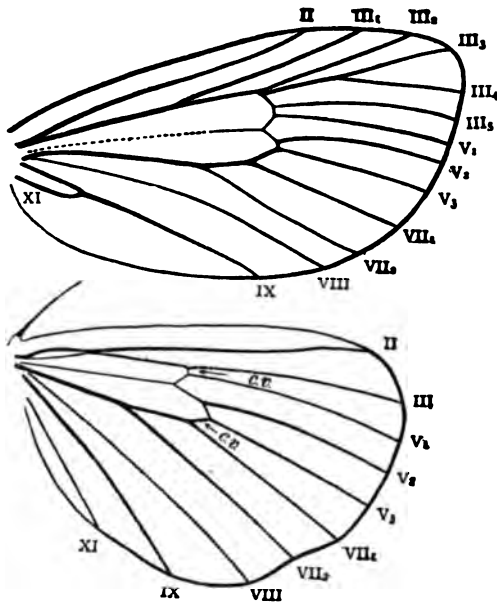


FIG. 16.—*Packardia*.

bending of the wing during flight, therefore any tendency to protect these tracheæ by a thickening of the membrane along their course would be beneficial and would result in the development of veins enclosing these tracheæ.

These veins at first extend in a transverse direction, and are thus obviously cross veins (Fig. 16, *c. v.*). But the result of

farther specialization is to round off the angles in the path of the tracheæ, as the angles in our roads are rounded off by carts. This process is continued until these cross veins become parts of longitudinal veins, and their true nature as cross veins is completely hidden. This is well shown by the connection existing between the third branch of media (vein  $V_3$ ) and cubitus. A study of the venation of *Castnia* (Fig. 15) shows conclusively that media is three-branched and cubitus only two-branched. Here the connection between vein  $V_3$  and vein VII is obviously a cross vein. But in every American moth and butterfly known to me, except perhaps *Hepialis* and *Micropteryx*, the union of these two veins is so complete that there is no hint of the fact that vein  $V_3$  is not a branch of vein VII. And in several families vein  $V_3$  has also become united with vein VII in a similar manner. The result is that cubitus (the median vein of many authors) is described as three-branched in some families and four-branched in others.

Two years after I had reached the conclusion that media is three-branched and cubitus only two-branched in the Lepidoptera, Spuler published a paper\* in which these facts are demonstrated in an entirely different way. As I did not publish my conclusions, the credit of the discovery belongs of course to Spuler. I wish merely to state that my conclusions were reached independently of that author's work, and by an entirely different method. I was led to the correct understanding of the relation of these veins by a study of existing generalized forms (especially *Hepialis* and *Castnia*); while Spuler's conclusions were based on a study of the ontogeny of certain butterflies. He found that in newly formed pupæ the trachea which later becomes enclosed by media is three-branched, while that one which is the precursor of cubitus is only two-branched. This is an interesting instance of the evidence of ontogeny confirming results obtained in an effort to determine the phylogeny of a group by the study of generalized forms.

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\* A Spuler.—Zur Phylogenie und Ontogenie des Flügelgeädters der Schmetterlinge. Zeit. für wissenschaftliche Zoologie, LIII.

Let us see how the facts regarding the changes of media can be used in taxonomic work.

First, the presence of the main trunk of media is an indication of a generalized condition. This at once throws light on the position of the Megalopygidæ, the Psychidæ, the Cossidæ, the Limacodidæ, and certain of the Zygaenina. These families are evidently much nearer the stem form of the Lepidoptera than are those families in which media has been lost.

It does not follow that these families should be classed together. For each one may represent a distinct line of development. The presence

or the absence of the base of media is a character that merely indicates the degree of divergence from a primitive type (see p. 43). The divergence in each case may be along a distinct line. It may be worth while to state in this connection that the families named above are nearly all of those of the Macrofrenatæ in which three anal veins are preserved in the hind wings, another character indicating a comparatively slight degree of divergence from the primitive type.

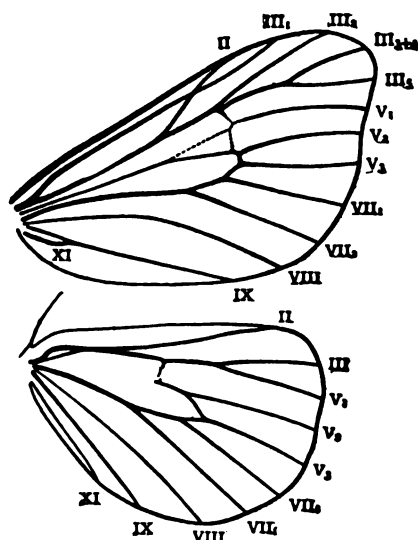


FIG. 17.—*Adoneta*.

Correlated with the abortion of the base of media is the coalescence of its branches with the adjacent veins. It follows from this that the extent to which this coalescence has gone is an indication of the degree of departure of a form from the primitive type. Compare, for example, the hind wings of *Packardia* (Fig. 16) with the hind wings of *Adoneta* (Fig. 17), two genera of the family Limacodidæ. In *Packar-*

*dia*, where a remnant of the base of media still persists, vein V<sub>1</sub> is merely connected with vein III by a cross vein. But in *Adoneta*, where the base of media of the hind wings is lost, vein V<sub>1</sub> has become consolidated with vein III for a considerable distance. It is obvious that in these respects, the loss of the base of media and the extent of the coalescence of veins III and V<sub>1</sub>, *Adoneta* is the more highly specialized of the two genera.

It often happens that after the abortion of the base of media the discal cell is traversed by a more or less distinct line or scar indicating the former position of this part of the vein. This scar is indicated in the accompanying figure of the wings of *Eacles* (Fig. 18) by dotted lines.

It will be observed that the branches of media are not continuous with the branches of this scar. There has been a migration of the proximal end of the remaining portion of each branch towards the vein from which it gets its supply of air. Frequently there remain short stumps, projecting into the discal cell from the discal cross vein, and continuous with the scar, at the points where the branches formerly emerged from the discal cell. These are indicated by the arrows in Figure 13, and are also shown in Figure 18. It will be readily seen that the extent to which this migration of the base of a branch has gone will serve as an indication of the degree of divergence of the form from a primitive type.\*

In connection with this part of the discussion a few words regarding the nature of the so-called discal vein are appropriate. It is evident that this is not a single cross vein extending from radius to cubitus; but it is made up of several distinct elements, and these elements may differ in different genera. There is a cross vein between radius and the first branch of media, and another between the third branch of media and cubitus (Figs. 16, 18, *c. v.*, *c. v.*). These extremes of the series forming the discal vein, however, have the appearance in many cases of being parts of longitudinal veins (Fig. 18);

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\* I wish here to acknowledge the assistance of Miss Clelia D. Mosher, who, while a student in my laboratory at Palo Alto, first worked out the relation of these stumps to the branches of media.

and in such cases have not been considered, heretofore, as parts of the discal vein. The intermediate portions of the discal vein may be merely the branches of media somewhat bent out of their primitive course. This condition is illus-

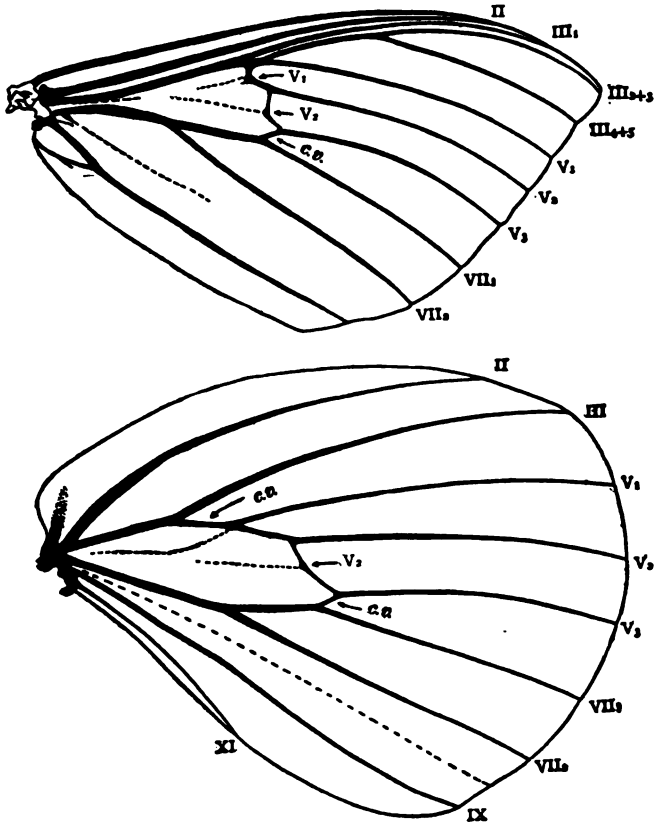


FIG. 18.—*Eacles*. The hind wing is enlarged more than the fore wing.

trated by the hind wings of *Packardia* (Fig. 16). Here the first branch of media has been drawn towards radius as a result of the change in the source of its air supply; and in a similar way the third branch of media, receiving a large part of its air from cubitus, is bent towards cubitus. In other



cases cross veins have been developed between the branches of media, and these form part of the discal vein; this is the case where there is an interpolated cell in the discal cell (Fig. 12). Sometimes a part of the discal vein may be looked upon as a trail indicating the path along which the base of a branch of media has migrated. An instance of this kind can be seen in the fore wings of *Eacles* (Fig. 18). Here that part of the discal vein lying between the stump which is marked  $V_1$  and radius is the path over which the base of vein  $V_1$  has migrated.

The union of vein  $V_1$  with radius and of vein  $V_2$  with cubitus after the abortion of the base of media is what would be expected. But in which direction would one expect the base of vein  $V_1$  to migrate? Occupying an intermediate position between radius and cubitus it may go either way. It is like a stream in the middle of a level plain, a trifle may change its course. And thus we find that in some families it migrates towards cubitus, making this vein apparently four-branched, while in other families it goes towards radius, leaving cubitus apparently three-branched.

This difference may be looked upon as a difference in kind of specialization, and is frequently of high value as indicating a dichotomous division of the line of descent. It is obvious that in a family, where vein  $V_2$  has migrated far towards cubitus and has thus established its chief source of air supply in that direction, it is not probable that genera will arise in which vein  $V_2$  is more closely united to radius than to cubitus. To resume the figure, the plain through which the stream is flowing is an elevated plateau; a pebble may determine which of two slopes it shall descend; but when well started down one, it cannot traverse the other.

This character, however, must be used with care. In families where the direction of the migration of the base of vein  $V_2$  has been firmly established, as in the Saturniidæ (Fig. 18), and in the Lasiocampidæ (Fig. 29), it is decisive. One need not hesitate a moment in determining to which of these two families a genus belongs. But there are other families in which the direction of this migration is not yet fixed; and here the character is of subordinate value.

Not only may the branches of one system of veins become joined to those of other systems as just described, but there are many forms in which two adjacent principal veins are coalesced to a greater or less extent. This occurs chiefly in the hind wings.

I will discuss the veins in regular order, beginning with costa. This vein is apparently wanting in the hind wings of most Lepidoptera, and but little can be said regarding the manner of its disappearance. It seems probable that in most cases it has simply become atrophied, the overlapping of the wings rendering it unnecessary or even undesirable. For when that stage in the development of the order was reached in which the two hind wings of each side overlapped to a considerable extent, was it not better that the costal margin of the hind wing should be flexible? There was no longer any need of a stiff margin, this part of the wing being supported during the downward stroke by the overlapping part of the fore wing; while a flexible margin would act as a valve to prevent the escape of the air between the two wings. The two wings in this way present a continuous surface. In many moths there is a thickening of the basal part of the costal margin; this I believe to be the remnant of costa.

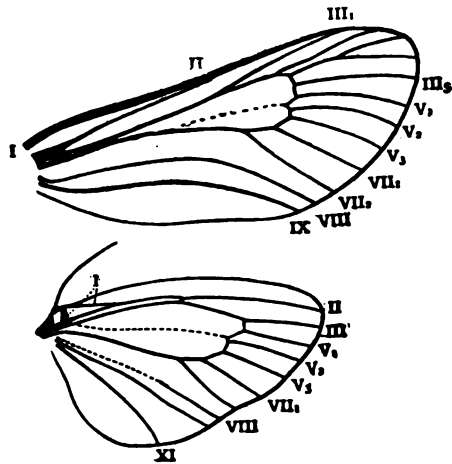


FIG. 19.—*Zygæna*.

But although it seems probable that in many cases the costa of the hind wings has simply faded out leaving cell I to function as this costal valve, there are cases in which this valve is a precostal development, the costa having moved

backwards and become consolidated with the subcosta. A good illustration of this is presented by the European genus *Zygæna* (Fig. 19). Here the costa and subcosta are distinct for a considerable distance, but become united into a single vein.

It will be observed that the basal portion of costa extends like a cross vein and forms a strong support for the frenulum. This part of costa is sometimes preserved when the remaining part is wanting. See figure of *Castnia* (Fig. 15).

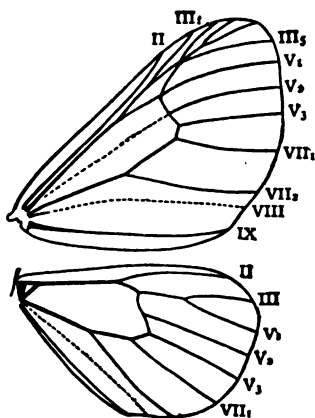


FIG. 20.—*Euphnessa*.

In most genera of the Geometridæ there is a faint indication of a remnant of costa extending from the humeral angle, at the base of the frenulum, to the subcosta, which is strongly angulated. The same thing is shown in *Euphnessa*, (Figs. 20, 21), which is probably a Geometrid genus.

In many of the Psychidæ a remnant of costa is preserved (Figs. 22, 23). Here subcosta and radius are united for a considerable distance; then they separate and subcosta soon becomes joined to costa for a short distance. In Figure 23 I have represented what I believe to be the course of these three veins, slightly separating them where they are coalesced.

That part of subcosta that lies between its separation from radius and its union with costa appears like an oblique cross vein; and had the short spur that represents the terminal part of costa been lacking, its true nature would not have been suspected. Does not this arrangement of the veins in the Psychidæ afford an explanation of the origin of the so-called intercostal vein which is characteristic of the Sphingidæ? See Figure 24. In many butterflies the base

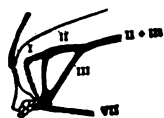


FIG. 21.—Humeral angle of hind wing of *Euphnessa*.

of costa of the hind wings is preserved. This is well shown in *Papilo* (Pl. II, 2). This vein has been observed and figured by many writers; but it has always been considered a precostal (*i. e.*, humeral) vein. But I believe it is essentially different from the humeral vein or veins of the *Lasiocampidæ*. The humeral veins of this family of moths are secondary developments; while the spur in the humeral angle of butterflies is a remnant of one of the primitive veins, the costa.

In the hind wings of many moths a coalescence of subcosta and radius also takes place to a greater or less extent. These two veins may be joined for a short distance, as in *Packardia*, (Fig. 16), or they may be merged into one for a considerable proportion of their length as in *Megalopyge*, (Fig. 25), and in the *Sesidæ*. Every degree of coalescence between these extremes exist.

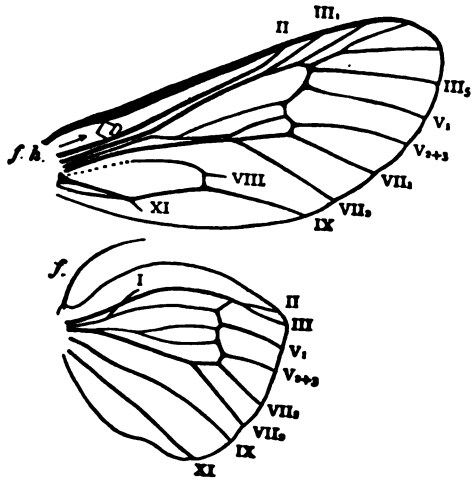


FIG. 22.—*Thyredopteryx*.

It has been customary in cases like the last to consider the subcostal vein wanting; but it is only necessary to count the branches of the principal veins to see that all are present; moreover, in most cases the two coalesced veins are separate for a short distance near the base.



FIG. 23.—Diagram of part of hind wing of *Thyredopteryx*.

There are, however, forms in which the basal part of radius is wanting. This condition is brought about in this way. First, something interferes with the growth of the basal part of radius, and this vein becomes weaker than the oth-

er principal veins. This stage is exhibited by *Prionoxystus*, (Fig. 12), in which radius of the hind wings still persists but is much weaker than the other veins, except media. Correlated with this weakening of radius is the formation of a cross vein between it and subcosta (Fig. 12, *c. v.*). This is an establishment of a new source of air supply for the distal portion of radius, and renders less necessary the basal portion of that vein. Sometimes the two veins are drawn together, and the

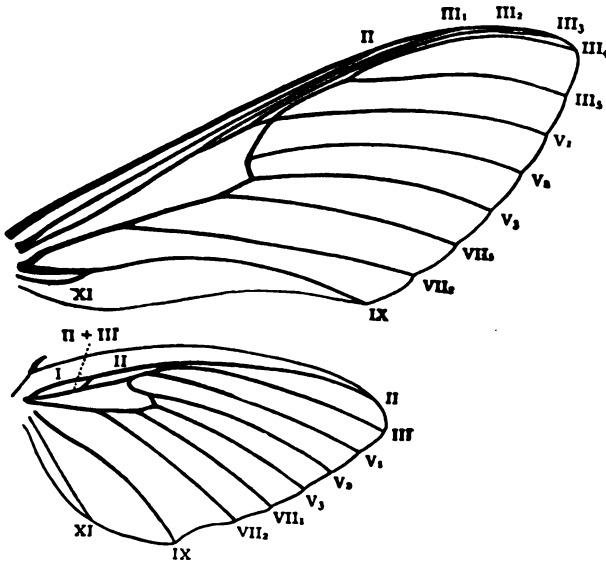


FIG. 24.—*Protoparce*.

coalescence extends in both directions from the point of first union, resulting in the form presented by *Megalopyge* (Fig. 25); but in other cases that portion of radius between the point of union and the base of the wing becomes atrophied. An approach to this condition is shown by *Acoloitthis* (Fig. 26).

In the fore wings where radius is branched, we often find an anastomosing of the branches. In this way are formed the accessory cells (Fig. 20). This anastomosing doubtless serves to strengthen the wing.

In the hind wings of all Lepidoptera, except *Hepialis* (Fig. 27) and *Micropteryx* (Fig. 28), all of the branches of radius are united into one. But the condition of radius in the two genera named shows that it is normally five-branched in the hind wings as well as in the fore wings.

In the discussion of media, given on a previous page, attention was called, so far as concerns its coalescence with other veins, merely to its branches; but the principal stem of this vein may become joined either to radius, as in the fore wing of *Castnia* (Fig. 15), or to cubitus, as in the fore wing of *Prionoxystus* (Fig. 12).

It will be observed that here is a character which is of value as indicating a dichotomous division of the line of descent.

I do not recall any instance where cubitus is coalesced with an anal vein to a marked degree, except in the Papilionidæ (Pl. II, Fig. 2); but the growing together of different anal veins is a very common occurrence. This condition is preceded phylogenetically by the formation of a cross vein. Such a vein exists between veins IX and XI of the fore wings of *Castnia* (Fig. 15), and between veins VIII and IX of *Thyridopteryx* (Fig. 22). Following this stage the two veins are drawn together, See veins IX and XI of the fore wings of *Thyridopteryx* (Fig. 22), and the same veins in *Megalopyge* (Fig. 25). Usually, however, when these veins are joined in this way, that part of vein XI beyond the point of union disappears, and vein IX presents the appearance of being forked towards the base. See *Adoneta* (Fig. 17).

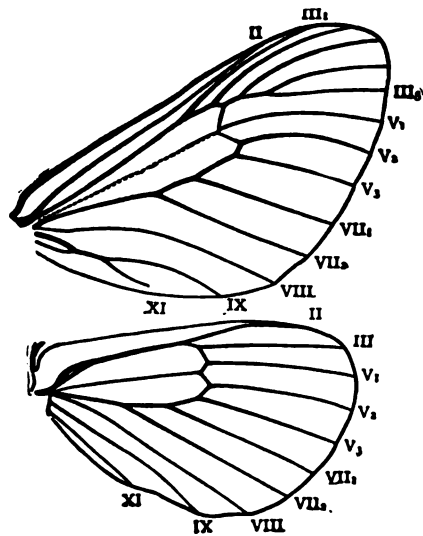


FIG. 25.—*Megalopyge*.

In the fore wings of the Psychidæ it frequently happens that the basal part of vein VIII disappears, and then vein IX appears to be forked outwardly (Fig. 22).

A good illustration of the coalescence of principal veins in another order of insects is presented by the dragon-flies (*Odonata*). Here veins III, IV and V are united into one from the base of the wing to the arculus. This coalescence is from the base of the wing outward, as is the coalescence of the main stem of media with either radius or cubitus in the Lepidoptera. But most instances of coalescence in the Lepidoptera

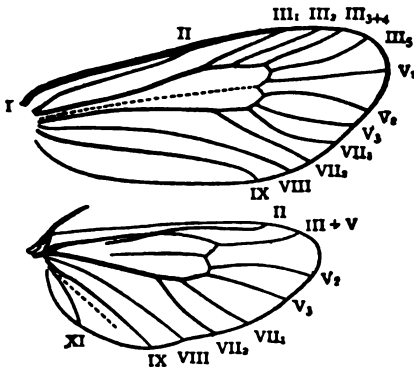


FIG. 26.—*Acoloithus*.

begin on the disc of the wing and extend in either direction. In the Diptera a third mode of coalescence is common. In this order it frequently happens that two longitudinal veins come together at their tips and unite, the coalescence proceeding from the margin of the wing towards the base.

The result is that a cell which normally opens

on the margin of the wing is closed at a greater or less distance before the margin; and the extent of this distance will be an indication of the degree of divergence from the primitive type.

The coalescence of two veins may be complete resulting in the reduction of the number of veins in the wing. This frequently happens especially with the branches of radius of the fore wings in the Lepidoptera. This vein is naturally five-branched; when a less number of branches occurs it is because the coalescence of some of the branches has proceeded to the margin of the wing.

The number of veins in the wing may be reduced, however, in another way: a vein may simply fade out. The most common instances of this kind in the Lepidoptera occur in the

anal areas of the wings. As these areas become narrowed (*i. e.*, specialized by reduction) one or two veins disappear.

The second branch of *media* is also a vein that is apt to disappear by atrophy; this occurs frequently in the Geometridæ.

The usual result of specialization of the wings of Lepidoptera is a reduction of the number of veins where any change in the number is made. But it is not always so; for new veins may appear. I have already described the formation of cross veins, where a new source of air supply is established, and preceding the coalescence of distinct

veins. In a somewhat similar way veins are formed in the basal part of cell I of the hind wings in the Lasiocampidæ. In these cases the humeral angle has become greatly extended (Fig. 29). This outgrowth of the wing, like all other parts, is abundantly supplied with tracheæ; and about

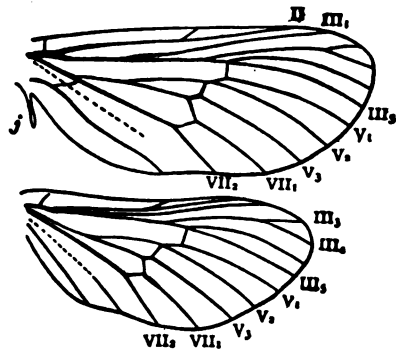


FIG. 27.—*Hepialis*.

some of the tracheæ have been developed veins which protect them by stiffening this area so that it will not bend and thus compress them. This stiffening of the area doubtless serves another function to be described later.

These veins, developed in the humeral angle of the wing, I designate as the *humeral veins*. They have been termed the precostal veins; but the determination of the fact that the so-called costa of Lepidoptera is really the subcosta, renders the name precostal inappropriate.

The joining together of the two wings of each side in many moths by means of a frenulum and a frenulum hook, is a well known characteristic. But the real nature of the frenulum has not been understood, neither has its taxonomic value been appreciated.



I was led to make a careful study of this part of the wing by the discovery that in *Hepialis* an entirely different method of uniting the two wings of each side has been developed. In this genus, and as I have since discovered in *Micropteryx* also, instead of the wings being joined by a frenulum, which is a bristle or a bunch of bristles borne by the hind wing, they are joined by a membranous lobe extending back from near the base of the inner margin of the fore wing (Fig. 27, 28, j).

To this lobe I have applied the name *jugum*.

When the wings of *Hepialis* are extended, the jugum projects back beneath the costal border of the hind wing, which,

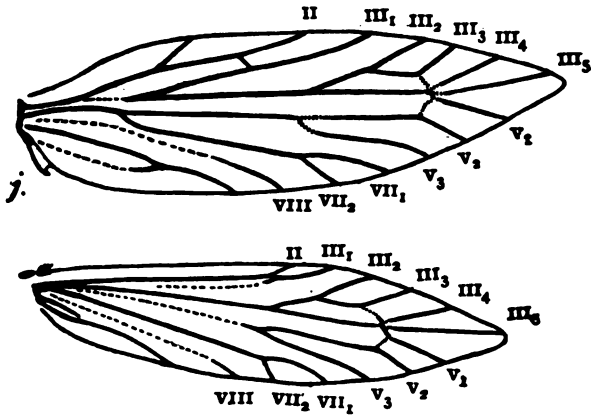


FIG. 28.—*Micropteryx*.

being overlapped by the more distal portion of the inner margin of the fore wing, is thus held between the two, as in a vice.

The discovery of the fact that there are two distinct modes of uniting the wings during flight suggests the inference that in the primitive Lepidoptera the wings were united in neither way. For it is not easy to see how one mode could have been developed from the other.

It is probable that in the primitive moths the mesothorax and metathorax were much more distinct than in the recent forms; and consequently the two pairs of wings were farther

apart than now. As the consolidation of the thoracic segments advanced, the wings were brought nearer and nearer together, till finally the development of a connecting organ was rendered possible.

Such an organ might be borne by the fore wings, or it might be borne by the hind wings. In some moths the specialization took the former direction; in others, the latter; and thus arose a division of the order.

This division I consider of subordinal value; and I have already proposed the names *Jugatae* and *Frenatae* for the suborders thus indicated.\*

Let us try to obtain an idea of the ways in which the jugum and the frenulum were developed. As to the jugum I have but little to offer beyond the suggestion that at first it may have been merely an adventitious lobe, or a slight sinuosity in the inner margin of the fore wing. If such a lobe should project beneath the hind wing ever so little it would tend to insure the synchronous action of the two wings, and thus offer an opportunity for natural selection to act.

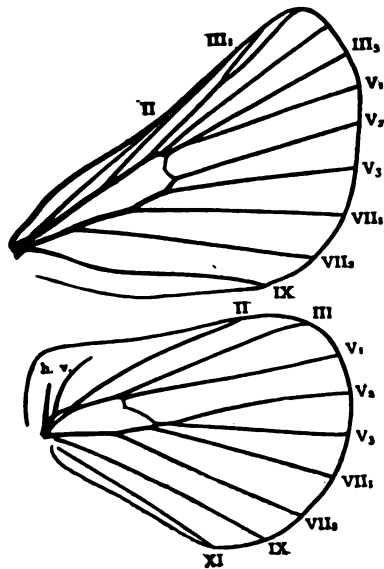


FIG. 29.—*Clisiocampa*.

The frenulum is a much more complicated organ. As a rule we find that in the female it consists of several bristles, while in the male it consists of a single, strong spine. If one of the bristles of the compound frenulum of the female be examined it will be found to be hollow, containing a single cavity. But when the frenulum of a male is examined it is found

\* Proc. Am. Ass. Adv. Sci., Vol. XLI (1892), p. 200.

to contain several parallel cavities. Evidently the frenulum of the male is composed of several bristles as is that of the female, but these bristles are grown together, forming a single strong spine. This can be easily seen by examining a bleached wing that has been mounted in balsam. Usually the cavities in the bristles contain air which renders them easily visible.

It is obvious, therefore, that the frenulum of the female exhibits a more generalized condition than does that of the male.

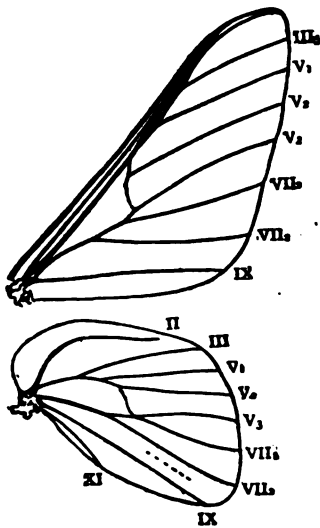


FIG. 30.—*Anisota*.

In some females the frenulum is so slightly developed that the bristles composing it are little more than hairs. This fact suggests that the primitive frenulum was developed from a bunch of hairs, clothing the base of the wing. Such a tuft of hairs projecting under the fore wing would tend in a slight degree to insure the synchronous action of the two wings; and as soon as these hairs had assumed this function the tendency of natural selection would be to strengthen them. In the female of *Prionoxystus* the frenulum consists of a series of bristles which vary in size from a short hair to a comparatively

long spine (Fig. 12, *f*). This throws much light on the development of this organ.

The extent to which the specialization of the frenulum has been carried is remarkable. In the males of some of the Psychidæ it is a strong spine nearly half as long as the hind wing (Fig. 22). In the Cymatophoridæ it is furnished with a knob at the tip. But the most remarkable feature of this specialization is the development of a membranous fold on the fore wings of males for receiving the end of the frenulum, and thus more securely fastening the two wings together.

This fold, or *frenulum hook*, is so well known that it is unnecessary to enter upon a detailed discussion of it. I will, therefore, merely record a few observations that I have made upon it. In all families in which I have observed it, it arises from the membrane of the wing near the base of cell I (Fig. 22), except that in *Castnia* it seems to have been pulled back so that it arises from the subcostal vein. The uniformity in the position of the *frenulum hook* indicates that it was developed before those families in which it exists had become separated phylogenetically. For if it had been independently developed in the different families there would probably have been a lack of uniformity in its position.

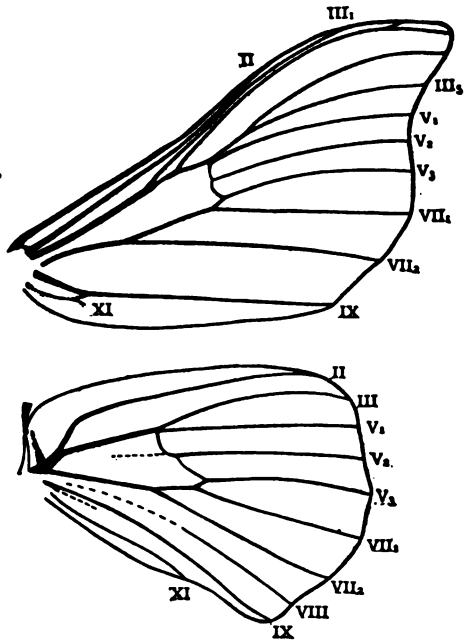


FIG. 31.—*Perophora*.

Some light is thrown upon the probable origin of the *frenulum hook* by the fact that in many females there is a tuft of curved scales projecting back from the base of cell I, and serving to hold the *frenulum* in place. In many moths there is also a tuft of scales projecting forward from the base of cell VII, which functions in a similar way.

In certain families of moths (*Saturniina*, *Lasiocampidæ*, and *Drepanidæ*) and in all butterflies there is neither a *frenulum* nor a *jugum*. But in other respects the wing characters of these moths and of butterflies agree quite closely with those

of the frenulum-bearing moths, and do not agree with the Jugatæ in their distinctive characters (*i. e.*, in an equal reduction of the two pairs of wings, and in having radius of the hind wings branched).

If the wings of one of these moths or of a butterfly be examined it will be seen that there is a large expansion of the

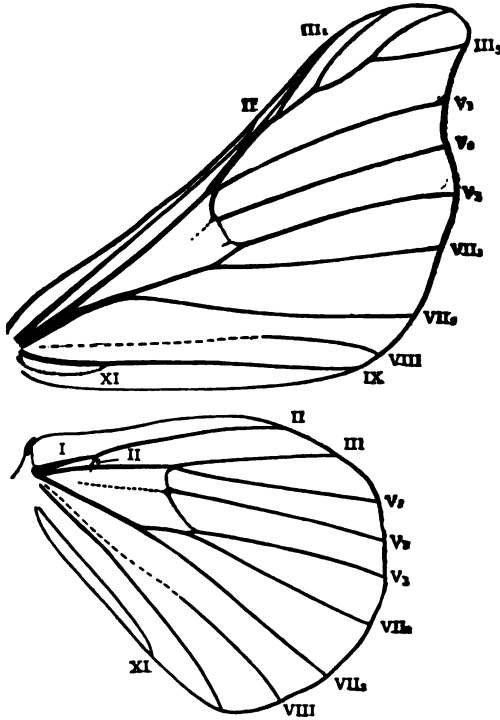


FIG. 32.—*Sericaria*.

humeral angle of the hind wings (Fig. 30, 14), which causes the two wings of each side to overlap to a much greater extent than they do in other Lepidoptera.

This extensive overlapping of the wings effectually insures their synchronous action without the aid of a frenulum, and I believe explains the loss of the frenulum. This theory is

supported by the fact that in the more generalized genera of the Saturniina (*Perophora* and *Sericaria*) where the humeral angle is not expanded to so great a degree as it is in the more specialized forms, there remains a rudiment of the frenulum, (Figs. 31, 32). And in the Drepanidæ where the frenulum is usually wanting, it persists in one sex in certain genera.

It is important that this expanded humeral angle should have a certain degree of stiffness if it is to perform the function of a frenulum. This has been obtained in some cases by a more or less diffused thickening of the membrane of the wing. Such a thickening is represented by the dotted portion in the figure of the hind wing of *Eacles*, (Fig. 18). In other cases the thickening takes place along a definite line and encloses a trachea; thus are formed the *humeral veins* of the Lasiocampidæ, (Fig. 29).

An interesting fact in connection with this abortion of the frenulum, is that in *Perophora* the rudiment of the frenulum of the male consists of a bunch of bristles. This is an excellent illustration of an organ which, in the course of its abortion, retraces the steps by which it was formed. In *Sericaria* the bristles composing the rudimentary frenulum in the male are still consolidated.

This modification of certain hairs on the costa of the hind wing into an organ whose function is to fasten the two wings together, is paralleled by the development of a row of hooks on the costa of the hind wings in the Hymenoptera and in the Aphididæ, which has a similar function. And the development of a jugum has taken place in the Trichoptera. In fact in several respects the Trichoptera and the Jugatæ resemble each other more closely than do the Jugatæ and the Frenatæ.

When a careful study is made of the wings of the two sexes of a species it often happens that a marked difference is found in them; and so far as I have observed the difference indicates a higher degree of specialization on the part of the male. It seems as if the female lagged behind the male in the race for perfection of organs. This is often shown in the degree to which the branches of the veins are consoli-

dated. But it is shown most markedly in the structure of the frenulum as already pointed out.

The explanation of this comparative lack of specialization of the wings in females is to be found largely, I believe, in the fact that the males seek their mates, while the females await the approach of the males. Many instances are well known (*Orgyia*, *Anisopteryx*, *et al.*) where the females have lost their wings through disuse while the males retain well developed wings. The only instance that I can call to mind where the reverse has occurred, is the case of *Blastopha-ga*. Here the male has no need of wings, as he finds his mate in the cavity of the fig in which he has been developed ; while the female must fly elsewhere to deposit her eggs in a suitable place.

The great difference in the habits of flight of the two sexes in many moths is well illustrated by the results of a series of experiments with trap lanterns which I conducted several years ago. Six lanterns were kept burning from spring to fall, and each day's catch was kept separate. The results have been partially tabulated by Mr. Slingerland, and I extract the following table from his report.\*

TABLE SHOWING THE NUMBER OF SPECIMENS OF EACH SEX OF TWO SPECIES OF FELTIA, CAPTURED WITH TRAP LANTERNS AT CORNELL UNIVERSITY IN 1889.

DATE.		<i>F. subgothica.</i>		<i>F. jaculifera.</i>	
		<i>Males.</i>	<i>Females.</i>	<i>Males.</i>	<i>Females.</i>
July	4 . . . . .				1
"	12 . . . . .	1			
"	17 . . . . .				1
"	21 . . . . .	2			
"	23 . . . . .	1			
"	26 . . . . .	1			
"	27 . . . . .	2			
"	28 . . . . .	1			
"	29 . . . . .	6			
"	30 . . . . .	2	2		
"	31 . . . . .	12	2		
Aug.	1 . . . . .	7	2		
"	2 . . . . .	19			2

\* Canadian Entomologist, Vol. XXV, 81.

DATE.		<i>F. subgothica.</i>		<i>F. jaculifera.</i>	
		Males.	Females.	Males.	Females.
Aug.	3	9	1	1	
"	4	17	3	1	
"	5	39	4	3	
"	6	5			
"	7	3			
"	8	5		1	
"	9	32	1		
"	10	7	1	4	
"	11	9	2		
"	12	5			
"	14	30	3	1	2
"	15	59	1	2	
"	16	42		1	
"	17	76	10		2
"	18	124	3	1	
"	19	161	9	5	
"	20	198	6		
"	21	160	19	1	1
"	22	108	6		
"	23	63	2		
"	24	122	10		
"	25	209	8		
"	26	110	7		
"	27	90	2		
"	28	93	3		
"	29	97	4		
"	30	53	2		
"	31	108	6		
Sept.	1	60	8		
"	2	65	2	1	
"	3	50			
"	4	87	4		
"	5	23			
"	6	37	2		
"	7	8			
"	8	16	3		
"	9	1			
"	11	1	2		
"	14	1			
"	16	2	1		
"	17	1			
"	18		1		
Total		2240	142	22	9

*Feltia jaculifera* is not a very common species at Ithaca and hence the results obtained with this species are not so important as those obtained with *Feltia subgothica*. This is our most common Noctuid ; and of the specimens captured (2,382



in all) more than 94 per cent. were males. It is not at all likely that this represents the difference in the numbers of individuals of the two sexes; it is much more probable that the difference is due to a greater activity on the part of the males.

While I believe that the greater specialization of the wings of the male is due to the greater activity of that sex, I confess that I am greatly puzzled by the fact that in no female of the *Macrofrenatæ* has a consolidated frenulum and a frenulum hook been developed.\* In other respects the females, as a rule, lag behind the males in their specialization only a short distance. But while the possession of a consolidated frenulum and a frenulum hook is attained by the males in the most generalized of living frenate moths, that stage is not reached by the females of the most specialized genera. Obviously there is a factor here that I have not discovered.

A similar lagging behind of the females is shown in a marked way in the specialization of the antennæ in the *Saturniidæ*. Here in the more generalized genera (*Coloradia* and *Hyperchiria*) the antennæ of the male alone are pectinate. In *Colosaturnia* the female has attained pectinate antennæ but unlike those of the male each segment bears only a single pair of pectinations. In the remaining genera of our fauna both sexes have pectinate antennæ and in each case each segment of the antennæ bears two pairs of pectinations; but the antennæ of the male are much more highly developed than are those of the female. If, as seems probable, the antennæ are organs of smell, and if, which also seems probable from certain well known experiments, the males in this family are guided to the females by the sense of smell, it is easy to understand the higher specialization of the antennæ of the males in this family.

In this discussion of the taxonomic value of the wings, I have confined myself chiefly to a study of the form of the wings, their venation, and the relation of the two pairs to each other. But I believe that even the clothing of the wings is of great taxonomic value.

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\*I have not studied the *Microfrenatæ* enough to be in a position to make generalizations regarding them.

If the scales of any of the more generalized moths be examined, they will be found to be long and narrow and scattered irregularly over the surface of the wing. On the other hand in the more specialized members of the order, as in most butterflies, the scales are much less hair-like, being short and broad; and they are arranged in regular overlapping rows. Evidently both the form of the scales and their arrangement upon the wing offer indications as to the degree of divergence from a primitive type of the insect bearing them.

More than this I am convinced that in some cases at least the form of the scales is characteristic of a particular line of development. One can determine, for example, without any doubt whether a moth belongs to the *Lasiocampidæ* or not by merely examining the scales of the wings.

I was impressed with the taxonomic value of the scales very soon after I began the systematic study of the *Lepidoptera* according to the method outlined in this essay. But the time at my disposal would not admit of my investigating this part of the problem in a satisfactory manner; and at my request the investigation has been undertaken by my colleague Professor V. L. Kellogg of the Leland Stanford Junior University.

Professor Kellogg is preparing an elaborate paper on this subject, which will be published soon after the appearance of the volume containing this one.

While the chief object which I have had before me is the indication of a method of taxonomic work, I hope this essay will be of value to entomologists in hastening the adoption of a uniform nomenclature of the parts of the wings of insects, and thus make easier the study of the relation of the different orders of insects to each other. In order that this nomenclature may be more complete I propose the following method of naming the cells of the wing; for we have as yet no system that is of general application.

The method I propose is, briefly, to designate each cell by the name or number of the vein that forms its front margin when the wings are spread.

The application of this system to the *Lepidoptera* is indicated by Figure 33.

In certain special cases special names may be desirable. Thus in the *Lepidoptera* the cells formed by the anastomosing of the branches of radius are commonly known as the *accessory cells*, which is a very convenient term. And cell III + V is universally known as the *discal cell*. In some of the more generalized moths a cell is formed within the discal cell by a forking of media: this has been termed the *interpolated cell* (Figs. 12, 22, 27).

In those orders where there are transverse veins, each of the cells between two longitudinal veins is divided into a series of

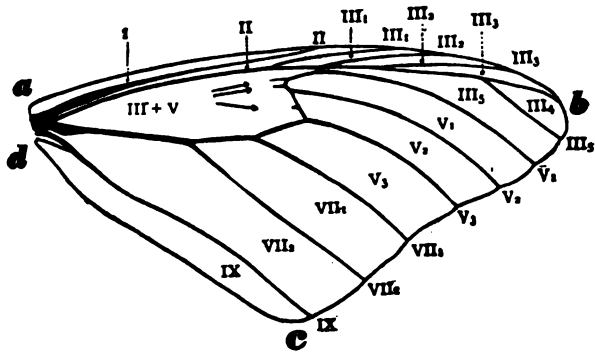


FIG. 33.—Fore wing of *Danais*, illustrating the nomenclature of the veins and cells. The numbers placed opposite the ends of the veins refer to the veins; the others, to the cells.

cells, and can be so designated. Thus the series of cells between veins III<sub>1</sub> and III<sub>2</sub> may be termed the first series of radial cells; and the members of such a series can be numbered. If one should speak of the peculiar form of the third cell in the second radial series, there need be no difficulty in determining the cell indicated, even by one who had not made a special study of the order to which the insect in question belongs. Heretofore it has been necessary for the student to learn a distinct nomenclature for each order, and in some cases for each family, studied.

In concluding this part of this essay I wish to refer to two curious methods of specialization that have interested me

greatly. In certain cases where the body of the insect has become greatly reduced in size, a reduction of the area of the wing membrane has taken place and correlated with this there has been a great expansion of the fringe of the wing. The best known examples of this are the narrow-winged Tineids, the Thysanoptera, and certain parasitic Hymenoptera. This kind of specialization seems possible only with minute insects, where the weight to be supported during flight is not great.

In a Tineid which I have studied the hairs composing the fringes of the wing are inserted in the lower side of the wing-membrane a short distance back from the edge of the wing; and the edge of the wing is stiffened above by strong overlapping scales. This arrangement renders the fringes rigid during the downward stroke of the wing, but admits of their depression during the upward stroke; a combination well adapted to facilitate flight.

The second method of specialization referred to above is the loss of the front wings in the Coleoptera and Euplexoptera. In these two orders the paraptera of the mesothorax have been developed into elytra, and have crowded out the front pair of wings. The function of flight has been relegated in this way to the hind wings.

This homology of the elytra of beetles with the tegulae of Hymenoptera and with the patagia of Lepidoptera was pointed out by F. Meinert long ago\* ; but Meinert's paper seems to have escaped the attention of entomologists almost entirely. It is referred to by C. Hoffbauer in his paper on the minute structure of the elytra.† But although Hoffbauer shows conclusively that the structure of the elytra resembles that of the pronotum and differs in every essential feature from that of the wings, strangely enough he does not accept the conclusion of Meinert.

Meinert also pointed out the fact that in many Coleoptera (*e. g.*, *Dytiscus*) rudiments of the front wings exist beneath the elytra.

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\* Entomologisk Tidskrift, 1880, 168.

† Zeit. Wiss. Zool., LIV, (1892), 579.

As to the cause of this strange specialization I can only conjecture that in the primitive Coleoptera the habits of the insects were such that the protection of the wings by elytra was of more importance than that the first pair should be functional ; cephalization was sacrificed in order that the remaining pair of wings might be protected. It may be that the primitive Coleoptera were wood borers, the only paleozoic remains supposed to be of beetles are borings ; or their habits may have been like those of the recent Carabidæ. In either case the wings would be in need of special protection.

### PART III.

#### A CONTRIBUTION TO THE CLASSIFICATION OF THE LEPIDOPTERA.

In this place I purpose to state briefly the conclusions that I have reached regarding the phylogeny of the families of the Lepidoptera. These conclusions are the results of an effort to read the record of the action of natural selection as recorded in the wings of these insects. Owing to the limited time at my disposal, but little attention has been given to the evidence presented by other parts of the body ; and for the same reason I have been able to study the Tineids, Tortricids, and Pyralids hardly at all. The following classification is, therefore, merely a provisional one ; and is put forth chiefly as a record of the results that I have obtained up to this time in applying the method outlined in the preceding pages.

I confidently expect, however, that the principal conclusions stated here will be confirmed by a study of other parts of the body ; for in Nature's court the testimony of different witnesses if rightly understood will agree. If any of the conclusions should prove to be incorrect, the fault will be found to lie with the translator and not in the record.

The fullness of the discussion that has already been given of the ways in which wings are modified will warrant considerable condensation in the following outline. I will first indicate the relations of the proposed divisions to each other by means of a table ; and will afterwards give fuller characterization of these divisions.

TABLE OF PROPOSED DIVISIONS OF THE LEPIDOPTERA.

- A. Suborder JUGATÆ.
  - B. *The Macrojugatæ* . . . . . Family HEPIALIDÆ.
  - BB. *The Microjugatæ* . . . . . Family MICROPTERYGIDÆ.
- AA. Suborder FRENATÆ.
  - B. *The Microfrenatæ*.
    - C. *The Tineids* . . . . . Superfamily TINEINA.
    - CC. *The Tortricids* . . . . . Superfamily TORTRICINA.
    - CCC. *The Pyralids* . . . . . Superfamily PYRALIDINA.
  - BB. *The Macrofrenatæ*.
    - C. *The Frenulum-conservers*.
      - D. Moths in which the reduction of the anal area of the hind wings precedes the reduction of the anal area of the fore wings. This group is not represented in the North American fauna. *Castnia* (Fig. 15) will serve as an illustration.
      - DD. Moths in which the reduction of the anal area of the fore wings precedes the reduction of the anal area of the hind wings.
        - E. *The Generalized Frenulum-conservers*.
          - F. Moths in which a great reduction of the subcostal cell of the hind wings is taking place.
          - G. Moths in which the anal veins of the fore wings anastomose so as to appear to be branched outwardly. (Fig. 25.)
            - Family MEGALOPYGIDÆ.
          - GG. Moths in which the anal veins do not anastomose in such a way as to appear branched outwardly.
            - Superfamily ZYGÆNINA (in part).
        - FF. Moths in which the subcostal cell of the hind wings is not greatly reduced.
          - G. Moths in which the anal veins of the fore wings anastomose so as to appear to be branched outwardly. (Fig. 22.)
            - Family PSYCHIDÆ.

- GG. Moths in which the anal veins do not anastomose in such a way as to appear branched outwardly.
- H. Family COSSIDÆ.
- HH. Family LIMACODIDÆ.
- EE. *The Specialized Frenulum-conservers.*
- F. DIOPTIDÆ.
- FF. *The Geometro-Bombycids and the Geometrids.*
- G. Family NOTODONTIDÆ.
- GG. Family BREPHIDÆ.
- GGG. Family GEOMETRIDÆ.
- FFF. *The Noctuo-Bombycids and the Noctuids.*
- G. Family CYMATOPHORIDÆ.
- GG. Family NOCTUIDÆ.
- Family LIPARIDÆ.
- Family AGARISTIDÆ.
- Family ARCTIIDÆ.
- FFFF. *Isolated Families of Specialized Frenulum-conservers.*
- G. Family SESIIDÆ.
- GG. Family THYRIDIDÆ.
- GGG. Family SPHINGIDÆ.
- GGGG. Superfamily ZYGÆNINA.
- CC. *The Frenulum-losers.*
- D. *The Frenulum-losing Moths.*
- E. Moths in which cubitus is apparently three-branched. Superfamily SATURNIINA.
- EE. Moths in which cubitus is apparently four-branched.
- F Family DREPANIDÆ.
- FF. Family LASIOCAMPIDÆ.
- DD. *The Skippers.*—"Butterflies" in which all of the branches of radius of the fore wings arise from the discal cell. Family HESPERIDÆ.
- DDD. *The Butterflies.*—Butterflies in which some of the branches of radius coalesce beyond the apex of the discal cell.
- E. Butterflies in which cubitus of the fore wings is apparently four-branched. Family PAPILIONIDÆ.

EE. Butterflies in which cubitus is apparently three-branched.

F. Butterflies exhibiting no tendency to abortion of the fore legs. Family PIERIDÆ.

FF. Butterflies exhibiting a marked tendency to abortion of the fore legs.

G. Family LYCÆNIDÆ.

GG. Family NYMPHALIDÆ.

A. SUBORDER JUGATÆ

This suborder includes those moths in which the two wings of each side are united by a membranous lobe, the *jugum*, borne at the base of the inner margin of the fore wings (Fig. 27, j), and in which the anal area of the hind wings is reduced while the radial area is not. The most available recognition character is the similarity in venation of the two pairs of wings; radius being five-branched in the hind wings as well as in the fore wings.

B. THE MACROJUGATÆ.

Moths of medium or large size. The mouth-parts are aborted, and correlated with this there persists a comparatively generalized condition of the wings, which is shown by the absence of a jugum plate. The larvæ are wood-borers. This division is represented by a single family.

Family HEPIALIDÆ.

BB. THE MICROJUGATÆ.

Moths of minute size. Mouth mandibulate, with both mandibles and maxillæ fitted for mastication. This is doubtless the most generalized form of mouth-parts preserved in this order. Correlated with the presence of functional mouth-parts, these moths show a higher specialization of wing structure than exists in the Hepialidæ; there being a plate-like organ at the base of the costa of the hind wings, the *jugum plate*, and a series of spines; both of which act with the jugum in assuring the synchronous action of the two pairs of



wings. (Fig. 28). The larvæ are leaf miners. This division is represented by a single family.

Family MICROPTERYGIDÆ.

AA. SUBORDER FRENATÆ.

This suborder includes those moths and butterflies in which the two wings of each side are united by a frenulum, borne at the base of the costal margin of the hind wings, or by a substitute for a frenulum, a large humeral area of the hind wings (see p. 88); and in which radius of the hind wings is reduced to an unbranched condition, while in the more generalized forms the anal area is not reduced. The most available recognition character is the dissimilarity in venation of the two pairs of wings, due to the unbranched condition of radius of the hind wings, while this vein in the fore wings separates into several branches. (See Figs. 10-33, except Figs. 27, 28).

B. THE MICROFRENATÆ.

Moths of small, often minute, size. The mouth-parts are usually functional. The anal area of the hind wings is not reduced, having three anal veins except in certain minute forms where a broad fringe has been substituted for the membrane of this area.

This division of the order is the Microlepidoptera of authors less the Micropterygidæ. But the statement made in many books that the presence of three anal veins in the hind wings distinguishes this group from the Macrolepidoptera is incorrect, for many of the Macros. possess this characteristic.

I believe, however, that the retention of the maximum number of anal veins in the hind wings by the Microfrenatæ is an index of an essential character of the group; while in the Macrofrenatæ, when it occurs, it is merely an indication of a slight degree of divergence from a primitive type. In other words, I believe that in the Microfrenatæ the tendency of natural selection is to develop that mode of flight which requires broadly expanded hind wings. While in the Macrofrenatæ the tendency has been at first in all groups and con-

stantly in some to develop a mode of flight requiring narrow wings.

This division of the order includes three superfamilies. I have nothing to add to their well known characteristics.

Superfamily TINEINA.

Superfamily TORTRICINA.

Superfamily PYRALIDINA.

#### BB. THE MACROFRENATÆ.

Moths usually of medium or large size ; a few are small. The anal area of the hind wings contains less than three anal veins except in some generalized families where the maximum number persists ; but in these families this character is usually correlated with rudimentary or aborted mouth-parts (see p. 48); and merely indicates a slight degree of divergence from a primitive type.

To this division of the order belong the most generalized of living Frenatæ ; but this division also includes the most specialized of all Lepidoptera. I therefore place it after the Microfrenatæ in an ascending series.

#### C. THE FRENULUM-CONSERVERS.

Under this head may be grouped those families of the Macrofrenatæ in which the two wings of each side are united by a frenulum. They are the families in which the tendency of natural selection is as a rule to conserve the frenulum, although in certain genera this organ may be greatly reduced.

The first separation of this group into divisions is indicated I believe by a difference in the order of reduction of the anal areas of the two pairs of wings. In one division (D), represented by *Castnia* (Fig. 15), the reduction of the anal area of the hind wings precedes the reduction of the anal area of the fore wings. In the other division (DD) the reverse is the case. As we have no representatives of the first division in the North American fauna, and as I have had but limited opportunity to study exotic forms, I will discuss only the second division, which includes those frenulum-conserving moths in which

the reduction of the anal area of the fore wings precedes the reduction of the anal area of the hind wings.

*E. The Generalized Frenulum-conservers.* — Moths in which the anal area of the hind wings retains three veins, and in which the base of media of one or of both pairs of wings is preserved. In all of these moths the second branch of media (vein  $V_2$ ) tends to become united with cubitus, thus forming a four-branched cubitus.

This is to a certain extent an artificial division, being based on characters that represent merely a degree of divergence from a primitive type. But it is really much more nearly a natural division than would seem at first sight. For if we omit those Zygænidæ that are included in it, it consists of four families, each of which is comparatively little removed from the stem form of the Frenatæ, and each represents a complete line of development. It is a grouping together of several short stems that arise near the base of the genealogical tree. In the case of the Zygænidæ included here we have to do with generalized members of a line of development which has reached in its more specialized forms as great a degree of divergence from the primitive type as has been attained by any members of the order.

I place but little weight upon the divisions of this group of families indicated below and in the table above. It is merely a convenient distribution based on recognition characters, and is not intended to represent affinities. For I believe each of these families represents a distinct line of descent, between which and any other line we at present know no connection except that of the common progenitor of all Frenatæ.

F. Moths in which a great reduction of the subcostal cell of the hind wings is taking place, the subcosta and radius being grown together to near the end of the discal cell. (Figs. 10, 25.)

G. Moths in which the anal veins of the fore wings anastomose so as to appear to be branched outwardly, (Fig. 25) The extremely generalized condition of these moths is shown by the slight reduction of the anal areas, there being three anal veins in both fore and hind wings, although veins IX and XI of the fore wings coalesce to a considerable

extent. The clothing of the wings is also in an extremely generalized condition, (see p. 93), and the larvæ too represent a generalized condition, having ten pairs of feet, three thoracic and seven abdominal.

The coalescence of subcosta and radius of the hind wings reminds us of what occurs in several of the more specialized families. But these moths cannot be regarded as representing the stem form of any of those families, as this coalescence takes place here before there is any reduction of the anal areas, while in the more specialized families referred to the anal areas are reduced first. This group is represented by a single family.\* There are two North American genera *Megalopyge* (*Lagoa*) and *Carama*.

Family MEGALOPYGIDÆ.

GG. Moths in which the anal veins of the fore wings do not anastomose in such a way as to appear to be branched outwardly. Three American genera, *Acoloithus* (Fig. 26), *Triprocris* (Fig. 10), and *Pyromorpha*, fall under this head. They will be discussed later, when the superfamily *Zygænina* is reached.

FF. Moths in which the subcostal cell of the hind wings is not greatly reduced.

G. Moths in which the anal veins of the fore wings anastomose so as to appear to be branched outwardly (Fig. 22). These are the Bag-worm Moths. They too show a generalized condition of the wings in the presence of three anal veins in both fore and hind wings; although in certain forms it is difficult to make out all of the anal veins in the fore wings, as the base of vein VIII is often wanting. The females have lost their wings entirely. The peculiar type of venation of the wings of these insects can not be regarded as representing the precursor of any other known type. I therefore look upon these insects as representing a distinct line of development. The group is represented by a single family.

Family PSYCHIDÆ.

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\* This family has been monographed by C. Berge. See *Farrago Lepidopterogica. Contribuciones al estudio de la Fauna Argentina y paises limetropes*. An. Soc. Arg. XIII. See also *Zool. Jahresbericht, 1882*. This monograph seems to have been overlooked by American writers.

GG. Moths in which the anal veins do not anastomose in such a way as to appear to be branched outwardly. This group includes two families, which so far as their wing-structure is concerned are more closely allied to each other than is either of them to either of the preceding families. In each of the two families included here there is frequently exhibited a marked tendency towards the abortion of radius of the hind wings.

H. Moths in which the branches of radius of the fore wings tend to anastomose, forming an accessory cell or cells (Fig. 12). The larvæ are wood borers. Family COSSIDÆ.

HH. Moths in which the branches of radius of the fore wings do not anastomose (Fig. 16, 17). The larvæ are "slug-caterpillars" and feed on the leaves of plants.

Family LIMACODIDÆ.

EE. *The Specialized Frenulum-conservers.* — Moths in which the anal area of the hind wings is reduced, having less than three anal veins, and in which that part of media which traverses the discal cell is usually wanting.

This division of the order is a very extensive one, including the greater number of the moths; it is represented in our fauna by thirteen groups, which are either of family or superfamily rank.

In several cases a family seems to be quite isolated; while in other cases several families can be brought together into a single larger group. I recognize two such groups. But in neither case does the group seem to be sufficiently homogeneous to be regarded as a superfamily; it must be regarded in each case as a provisional arrangement, which will be of use until the affinities of the families are better understood. These two groups are defined under FF and FFF below. Under F and FFFF are grouped the isolated families.

F. The family Dioptidæ represented by the genus *Phryganidia*, which occurs in California, seems to represent a distinct line of development. For it presents a combination of characters that sharply distinguishes it from all other known members of our fauna. The anal area of the fore wing is reduced, vein IX alone being retained (Pl. III,

Fig. 6). In the hind wings veins IX and XI are well preserved and the distal part of vein VIII is represented by a slight thickening of the membrane. The second branch of media in both wings nearly retains its primitive position; in fact it can not be said that a tendency to migrate in either direction has been established, although the base of media is lost. In the fore wings the third branch of media, and in the hind wings both the first and third branches of this vein, have become consolidated in each case with the adjacent vein to a remarkable extent. Here is a high degree of specialization in one direction correlated with a comparatively generalized condition of certain other characters. Although subcosta and radius of the hind wings are closely parallel, they are distinct. The clothing of the wings is extremely generalized, consisting chiefly of narrow scales, with a single notch at the extremity, and scattered irregularly over the surface of the wing. The larvæ resemble those of some of the Notodontidæ.

Family DIOPTIDÆ.

FF. *The Geometro-Bombycids and the Geometrids.*—Under this head I group three families that have been quite widely separated heretofore. This group includes those families of the Specialized Frenulum-conservers in which the base of the second branch of media (vein V<sub>2</sub>) tends to migrate towards radius; or in other words, those Specialized Frenulum-conservers in which the tendency is to form a three branched cubitus. (See p. 76 for a discussion of the importance of this character.)

G. Moths resembling Noctuids in their general appearance, having heavy, strong wings; but readily distinguished from that family by the direction of the migration of the base of vein V<sub>2</sub>. In this family there seems to be but little if any tendency to specialization of the humeral angle of the hind wings. (Compare with the Geometridæ below.)

Family NOTODONTIDÆ.

GG. Of this group I know only a single species, *Brephos infans*. I therefore hesitate to characterize it. I believe, however, that this represents its natural position.

Family BREPHIDÆ.

GGG. Moths in which the wings are usually delicate and very finely scaled. There seems to be a marked tendency in this family to a specialization of the humeral angle of the hind wings, and correlated with this a tendency towards the reduction of the frenulum, especially in the females of certain genera. This tendency, however, is a much later development than the corresponding tendency with the Frenulum-losers. A marked indication of the specialization of the humeral angle of the hind wings which is exhibited by most genera of this family is a bending forward into it of the basal part of the subcosta and an elongation of the frenulum brace.\* Both of these features are well shown by *Euphenessa* (Figs. 20, 21), which doubtless belongs to this group, although it is commonly placed elsewhere. Family GEOMETRIDÆ.

FFF. *The Noctuo-Bombycids and the Noctuids*.—The members of this group can be recognized by a tendency of the base of vein  $V_2$  to migrate towards cubitus, and thus form a four-branched cubitus, and an absence of the peculiar characteristics distinctive of any of the families grouped under the next division (FFFF).

G. Here belongs a small family, which, although apparently closely allied to the Noctuidæ, exhibits striking peculiarities of development. There is no tendency towards a uniting of the subcosta and radius of the hind wings (Pl. III, 4), a tendency shown in all other families of the Noctuo-Bombycid division. The migration of the base of vein  $V_2$  is more marked in the hind wings than in the fore wings, where it nearly or quite preserves its primitive position. And the union of vein  $V_1$  of the hind wings with radius is by means of a comparatively long cross vein, so that veins III and  $V_1$  appear to separate before the apex of the discal cell. In the males the tip of the frenulum is knobbed. The genus *Leptina* commonly placed in this family belongs to the Noctuidæ.

Family CYMATOPHORIDÆ.

GG. The four families that follow I have not yet studied

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\* By the term *frenulum brace* I designate a sclerite situated on the costal margin of the wing between the base of the frenulum and the base of the wing.

sufficiently to warrant my expressing any views as to their relationships to each other. In the Arctiidæ we find the most marked tendency to the reduction of the subcostal cell of the hind wings, subcosta and radius being consolidated in some genera for the greater part of their length. (Pl. III, 1).

Family NOCTUIDÆ.

Family LIPARIDÆ.

Family AGARISTIDÆ.

Family ARCTIIDÆ.

FFFF. *Isolated families of specialized Frenulum-conservers.*  
—The families that are grouped together here agree with the Noctuids and the Noctuo Bombycids in the direction of the migration of vein  $V_2$ , the tendency being to form a four-branched cubitus. But each of the following families exhibit striking peculiarities of specialization which isolate it from all of the others as well as from the preceding group of families.

G. The clear-winged moths are placed here provisionally, although I believe that their true position is among the Microfrenatæ. But as I have studied them and the Microfrenatæ only superficially, I will not presume to make so radical a change. In this family there is a high specialization of the wings, although the anal area of the hind wings in many cases retains three anal veins. This is a combination of characters not found elsewhere in the Macrofrenatæ, but is quite characteristic of the Microfrenatæ.

Family SESIIDÆ.

GG. The Window-winged Moths exhibit a type of wing venation not seen elsewhere among moths. The most striking feature of it is expressed by saying that all of the branches of radius of the fore wings are preserved, and all arise from the discal cell (Plate III, Fig. 2). A similar type of venation is exhibited by the Hesperidæ (Plate III, Fig. 1). Whether this similarity has arisen independently, or whether it indicates a closer genetic relationship than has been assigned to these families heretofore I will not presume to say, with my present knowledge. The fact that in the Hesperidæ the frenulum brace is well preserved, may have some bearing on the settlement of the question.

Family THYRIDIDÆ.



GGG. The Hawk-moths can be recognized by the well known form of their wings, and the presence of what has been termed an intercostal vein (Fig. 24). If I am correct in my interpretation of the homology of this vein, (see p. 78), the family can be characterized as those specialized Frenulum-conservers in which the base of costa of the hind wings is preserved and is remote from the costal border of the wing, and in which subcosta of the hind wings is consolidated with radius for a distance and then separates from radius and joins costa. This arrangement of the veins is quite different from that which exists in *Zygæna*, (Fig. 19), where also costa of the hind wings is preserved. It more closely resembles that of the silk worm, *Sericaria*! (Fig. 32.)

Family SPHINGIDÆ.

GGGG. I place the Zygænidæ last in this group of isolated families because it is among them that we find the most highly specialized representatives of the frenulum-conserving Lepidoptera, (*Cosmosoma*, *Syntomis*, Fig. 11). On the other hand certain genera, *Triplocris* (Fig. 10) and *Pyromorpha* present a remarkably generalized condition of wing structure. The range of variation is greater than I have observed in any other family or superfamily. In the more specialized forms a greater degree of cephalization of the powers of flight has taken place than occurs elsewhere in the order. And with this cephalization there seems to be correlated a lengthening of the fore wings and a narrowing of the basal part of the area lying between radius and cubitus of these wings. This narrowing of this area appears even in our most generalized forms, in which the discal cell of the fore wings can be well described as petiolate. Another characteristic of the Zygænina is the extent of the coalescence of the subcosta and radius of the hind wings. A somewhat similar coalescence occurs in certain genera of the Arctiidæ; but it takes place earlier (*i. e.*, in more generalized forms) in the Zygænina, and is carried farther than in the Arctiidæ. The Zygænidæ form a superfamily. The relationship of the families composing this superfamily have not been worked out. The American genera, so far as they are known to me, differ markedly from

*Zygæna* in the structure of the humeral area of the hind wings. In none of them is costa preserved. The American genera included here are *Acoloithus*, *Triplocris*, *Pyromorpha*, *Harrisina*, *Euchromia*, *Dahana*, *Didasys*, *Lycomorpha*, *Anatolmis*, and *Cosmosoma*. Of *Euchromia* I have studied only exotic forms; *Horama* and *Erruca* are unknown to me, but probably belong here also. The position of the Ctenuchidæ I have not determined. Superfamily ZYGÆNINA.

## CC. THE FRENULUM-LOSERS.

This division of the order includes those families of Lepidoptera in which the frenulum has been supplanted by a greatly extended humeral area of the hind wings, (see p. 88). In some of the more generalized forms a rudimentary frenulum persists, (*Sericaria*, *Perophora*); in others it has been retained by the male (*Drepana*). This division includes three groups of families; the Frenulum-losing Moths, the Skippers (Hesperidæ), and the Butterflies.

D. *The Frenulum-losing Moths.*

E. Moths in which cubitus is apparently three-branched.

Superfamily SATURNINA.\*

\* The following expresses my views regarding the affinities of the members of this superfamily :

A. Moths in which the base of costa of the hind wings is preserved remote from the costal border of the wing. This is shown by the presence of an "intercostal vein" (*Sericaria*, Fig. 32.) (See p. 78.) Frenulum preserved in a rudimentary state.

Family BOMBYCIDÆ.

AA. Moths lacking an "intercostal vein." (These are the true Saturnians.)

B. Generalized Saturnians. In these vein  $V_2$  retains its primitive position, midway between radius and cubitus; and there are three anal veins in the hind wings, the distal part of vein VIII being preserved (Fig. 31.) Frenulum preserved in a rudimentary state.

Family PEROPHORIDÆ.

BB. More Specialized Saturnians. Vein  $V_2$  of the hind wings apparently a branch of radius (Fig. 30); anal area of hind wings with not more than two veins, vein VIII having been lost; frenulum entirely superseded by a greatly extended humeral area.

C. Antennæ of both sexes with only a single pair of pectinations to each segment.

Family HEMILEUCIDÆ.

EE. Moths in which cubitus is apparently four-branched.

F. Humeral angle not strengthened by humeral veins. The frenulum is retained by the males in some genera. The North American forms represent three genera: *Drepana*, *Prionia*, and *Dryopteris*. Family DREPANIDÆ.

FF. Humeral angle strengthened by the development of one or more humeral veins. There are eight North American genera: *Quadrina*, *Gloveria*, *Thauma*, *Clisiocampa*, *Heteropacha*, *Artace*, *Tolype*, *Gastropacha*. Family LASIOCAMPIDÆ.

DD. *The Skippers*.—These are day-flying Lepidoptera, which resemble butterflies in usually holding their wings erect when at rest. They can be recognized by the peculiar venation of the fore wings, in which all of the branches of radius are preserved, and all arise from the discal cell. Although the frenulum is lost, the frenulum brace (see p. 106) is well preserved in some genera. See discussion of the Thyrididæ (p. 107) and compare the figures Plate II, Fig. 1, and Pl. III, Fig. 2. Family HÆSPERIDÆ.

CC. Antennæ of at least the males with two pairs of pectinations to each segment, excepting the terminal segments in some.

D. Antennæ of males pectinate for a little more than half their length. Family CERATOCAMPIDÆ.

DD. Antennæ of males pectinate throughout.

Family SATURNIDÆ.

BOMBYCIDÆ.—The superficial resemblance between this family and the next as shown by the single genus of each known to me (*Sericaria* and *Perophora*) is very striking. But a study of the structure of the wings shows marked differences (Figs. 31, 32). Note differences in the method of coalescence of the branches of radius of the fore wings, in the course of subcosta of the hind wings, and in the presence of an "intercostal vein."

*Sericaria* appears to represent a line of descent quite distinct from the true Saturnians as represented by the American forms. Do the "intercostal vein" of *Sericaria* and the caudal horn of its larva have any genetic connection with the similar structures in the Sphingidæ? This question suggests the desirability of a study of other Asiatic forms allied to *Sericaria*. It should be remembered that although *Sericaria* and the Sphingidæ belong to widely separated divisions of the order, *Sericaria* stands near the foot of one of them, being very generalized in structure.

PEROPHORIDÆ.—I propose the establishment of this family to receive the genus *Perophora*, the most generalized of the American Saturnians.

DDD. *The Butterflies*.—If we remove the Hesperidæ from this division of the order as indicated above, the butterflies form a well defined group. It contains, however, two distinct lines of descent which separated very early in the history of the group. In one, after the abortion of the base of media, vein V<sub>1</sub> migrated towards cubitus, forming a four-branched cubitus; in the other, this vein migrated in the opposite direction. There was also a difference in the order of the reduction of the anal areas of the two pairs of wings. See page 44 for a discussion of the importance of this character.

E. Butterflies in which cubitus is apparently four-branched; and in which the anal area of the hind wings is more reduced than the anal area of the fore wings. In the fore wings all three of the anal veins are at least partially preserved, while in the hind wings there is only a single anal vein. Pl. II, Fig. 2.

Family PAPILIONIDÆ.

EE. Butterflies in which cubitus is apparently three-branched; and in which the anal area of the fore wings is

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I infer from the figure and description of *Lacosoma* that it also belongs here. *Perophora* has been classed in the Psychidæ merely because its larva is a case-bearer. But it presents no affinities to the Psychidæ, beyond belonging to the same suborder, even in larval habits. The case of the larva of *Perophora* is of an entirely different type from that characteristic of the Psychidæ.

HEMILEUCIDÆ.—This family represents a distinct line of development within the Saturniina, which separated from the branch giving rise to the Ceratocampidæ and Saturniidæ before the origin of the peculiar form of antennæ characteristic of these families. For although the Hemileucidæ lack this peculiar specialization, the extent of the migration of vein V<sub>1</sub> that has taken place in this family, indicates a higher degree of specialization in another direction than exists in any of the Ceratocampidæ or in the lower genera (*Coloradia* and *Hyperchiria*) of the Saturniidæ. This family is represented in this country by two genera, *Hemileuca* and *Pseudohazis*.

CERATOCAMPIDÆ.—I have nothing to add to the well known characteristics of this family. There are five North American genera: *Citheronia*, *Eacles*, *Sphingicampa*, *Anisota*, and *Dryocampa*.

SATURNIIDÆ.—We have eight genera representing this family; these are, beginning with the most generalized: *Coloradia*, *Hyperchiria*, *Calosaturnia*, *Telia*, *Actias*, *Saturnia*, *Attacus*, and *Samia*.

more reduced than the anal area of the hind wings, the former having a single anal vein, the latter two, Pl. II, Fig. 3. This group includes three families.

F. Butterflies exhibiting no tendency to abortion of the fore legs. Family PIERIDÆ.

FF. Butterflies exhibiting a marked tendency to abortion of the fore legs.

G. Family LYCÆNIDÆ.

GG. Family NYMPHALIDÆ.

The most important innovation in the classification of butterflies proposed above, after the removal of the skippers, is the dismemberment of the Family Papilionidæ of authors, and the raising of the Pierinæ to family rank. I propose this change unhesitatingly; for it seems to me that nowhere within the Frenatæ is a dichotomous division of a line of descent more clearly indicated than in this case.

If I am right in my conclusions the much mooted question as to which is the more highly specialized, the Papilionidæ or the Nymphalidæ, disappears. For we have to do, not with two elements of a single series, but with the tips of two distinct lines of descent, each of which represents the highest degree of specialization of its line.

It is difficult for one who has adopted the commonly accepted classification of the butterflies to realize the great extent of the gap that separates the Papilionidæ (as limited here) from the other families of butterflies. The branching off of the Papilionidæ took place long before butterflies assumed their present form. At the time when it occurred there had been no reduction of the anal areas, and vein  $V_1$  had not begun its migration towards either radius or cubitus. This is as generalized a condition of wing structure as exists in any of the living Frenatæ.

The division between the Pieridæ on the one hand and the Lycænidæ and Nymphalidæ on the other is also well marked. If we compare the Pieridæ with the Lycænidæ, the more generalized of the last two families, we find that the Pieridæ exhibit a much greater specialization of wing structure (as shown by the extent of the consolidation of vein  $V_1$  with

radius) than do the *Lycænidae*; but the *Pieridae* do not exhibit that specialization by reduction of the fore legs which is characteristic of the *Lycænidae* and *Nymphalidae*. In the *Nymphalidae* we find not merely the extreme of the reduction of the fore legs, but an even greater specialization of the wings than exists in the *Pieridae*.

ITHACA, N. Y.,  
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