WING STRUCTURE OF LEPIDOPTERA AND THE PHYLOGENETIC AND TAXONOMIC VALUE OF CERTAIN PERSISTENT TRICHOPTEROUS CHARACTERS.

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I. INTRODUCTION.

It is agreed that the insects constituting the two orders Trichoptera and Lepidoptera respectively are closely related genetically. All insects included in these orders have the same general and characteristic type of venation, which in the more primitive forms closely approaches the hypothetical primitive type as figured by Comstock. It is the problem of determining where the line of division shall be drawn between Lepidoptera and Trichoptera which presents difficulties. According to the usually accepted classification, the Micropterygidæ are regarded as the most primitive group of Lepidoptera, from which all the other Lepidoptera have been derived. This group more closely resembles in venation and mode of uniting the fore and hind wing in flight the more generalized of the Trichoptera than it does any other group of insects, evidently approaching the stem form from which both groups have been derived. On the basis of certain common and characteristic features in venation, and the identical structure of the fibula in both, Comstock ('18) removes the Micropterygidæ from the Lepidoptera, confirming his conclusion by the results of Dr. T. A. Chapman's studies of pupæ, and makes them one suborder of the Trichoptera, the Micropterygina, the members of Trichoptera as usually recognized constituting the other suborder, the Phryganeina.

In addition to the Micropterygidæ, there is another group of moths, the Nepticulidæ, the more generalized members of which possess a fibula identical in structure with that of the

Micropterygidæ and the generalized Trichoptera,* and a pupa resembling that of the Microptergyidæ. The venation of the Nepticulidæ (Braun, '17) shows highly specialized features. It resembles most closely the venation of some of the Hydroptilidæ, but shows extreme anastomosis of main veins and absence of cross-veins. It differs from that of Hydroptilidæ chiefly in the few points in which the Nepticulidæ approach the usual type of venation in the frenate Microlepidoptera with reduced venation. The existence of this group, which shows undoubted trichopterous affinities, further complicates the question of the true relationship existing between the Trichoptera, the Micropterygidæ, the Nepticulidæ, the Hepialidæ, and the frenate Lepidoptera.

The discovery of another family, the Prototheoridæ (Meyrick, Annals South African Museum, XVII, 17, 1917), with characters intermediate between the Micropterygidæ and the Hepialidæ, would seem to make it impossible to place the Micropterygidæ and Hepialidæ in different orders.

In two related groups, any adaptation for a particular function may have been handed down from the common ancestor of the two, or it may be a similar modification of an homologous structure arising independently in each group, because of the same inherent tendencies in each, or the adaptations serving the same purpose may be developments of entirely different structures in the two groups. The two former conditions indicate community of descent and closeness of relationship; the third the phylogenetic divergence of the two groups. The same principles may be applied in the analysis of the entire structure of the groups whose true relationship is to be determined. If it can be shown, that the more primitive members of one group having many characteristics in common with the primitive members of another group and thus appearing more closely related to them than to any other group, show the beginning of divergence in structure from that other group, and these modifications can be consistently traced in the same direction through the more specialized members of the first group, in my opinion the point where the two groups begin to diverge, that is, the point where the distinctive characteristics of a group originate, is the logical place to make a taxonomic

* The term Trichoptera is used in this paper in its commonly accepted sense, not including the Micropterygidae.

division, even though an apparently wider gap may exist somewhere between two divisions of a group, due to incomplete preservation of connecting forms or insufficient knowledge on our part.

In the present paper, the relative value of those factors indicating community of descent and relationship of the insects constituting the Trichoptera and Lepidoptera and those indicating divergence is considered in its bearing on the question of classification.

With regard to the taxonomic problem involved, the question is essentially this: Are certain characteristics possessed by the Micropterygidæ in common with the Trichoptera of such taxonomic importance as to necessitate the conclusion that the Micropterygidæ are trichopterous insects or are these characteristics merely retained as a common inheritance, later to undergo far-reaching modifications which can be traced back to the Micropterygidæ.

Certain characters which are possessed in common by the Micropterygidæ and Trichoptera and which seem sharply to separate the Micropterygidæ from frenate Lepidoptera, will be shown to undergo far-reaching modification and in this modified form to persist in many of the comparatively primitive groups of the frenate Lepidoptera. The fact that the course of such modification can be traced makes it evident that the gap between the Micropterygidæ and the remaining Lepidoptera is not as wide as is sometimes supposed. This fact, and the fact that certain acknowledged lepidopterous characters originate in the Micropterygidæ, necessitate the conclusion that the Micropterygidæ are lepidopterous insects.

II. Wing Structure.

The structure of the wings presents the most obvious and available characters for the study of the phylogeny and taxonomy of the Lepidoptera and Trichoptera. The following discussion of the structure of wings of Lepidoptera deals with the modification and disappearance of trichopterous characters and with the origin of some distinctively lepidopterous characters. The data are presented under (a) venation, (b) mode of insuring synchronous action of fore and hind wings, (c) distribution of fixed hairs.

(*a*) *Venation.*

Certain striking characteristics of venation are held in common by the more generalized Trichoptera, such as *Rhyacophila* and by the more generalized of the Micropterygidæ. These characteristics have been enumerated by Comstock (The Wings of Insects, 1918, p. 317). In fact, the resemblance is so close that the only essential difference to be noted is that in Micropterygidæ media of both wings has been reduced to a three-branched condition, apparently by the coalescence of M_3 and M_4, while in *Rhyacophila* M_3 and M_4 are separate in the fore wing, although united in the hind wing. This identity of characteristics is shared by no insect not belonging to Micropterygidæ or Trichoptera. That it is possible to trace the modification of these trichopterous characters and their transformation into what are commonly recognized as the usual lepidopterous characters, such as are found in the frenate Lepidoptera, will be shown from evidence derived from the Micropterygidæ themselves, the Nepticulidæ, the more primitive frenate Lepidoptera, and the Hepialidæ.

The forms for study of venation in the more primitive Lepidoptera have been chosen because they show, besides the preservation of media, certain characters—such as the costal spines on the hind wing, absence of frenulum in the female, fixed hairs on the wings and folded maxillary palpi—all of which indicate a generalized condition.

In the Micropterygidæ veins *Cu* and *1st A* of both fore and hind wing coalesce at the base of the wing; from their point of separation *Cu* extends obliquely across the wing toward media, then bends and extends longitudinally to the margin. In the hind wing, the point of separation of *Cu* and *1st A* is nearer the base than in the fore wing. A short cross-vein, the posterior arculus, connects media with the longitudinal part of *Cu*, forming with the base of media, a serial vein in the fore wing. The presence of this condition in *Mnemonica* and in *Rhyacophila* is pointed out by Comstock in his book "The Wings of Insects," where wings of both are figured together with figures of the tracheation in the base of the wings of *Mnemonica*, which confirm the homologies of the veins as determined from a study of adults. In so far as published figures of other genera of the Micropterygidæ show the details

of venation at the base of the wings, they indicate that these conditions are common to all members of the family, although not without modification which may tend to obscure these characters. That such modification does take place in the Micropterygidæ, is shown by an examination of the wings of *Epimartyria* (Fig. 1), which genus, since it precedes the appearance of the tongue, must be regarded as a more primitive genus than *Mnemonica*. In the fore wing, the configuration of these veins is essentially that of *Mnemonica*. In the hind wing, *Cu* extends straight to the margin from its point of separation from the *1st A*, that is, the "oblique" part of *Cu* has become so extremely oblique as to be in a line with the longitudinal part of *Cu*. As is to be shown presently, this differs in no way from the course of *Cu* of the hind wing in certain undisputed Lepidoptera. In *Prodoxus*, most of the tracheae are preserved in the extreme base of the wings. Figure 2 shows the more general features of the venation, with wavy lines representing tracheæ; Figure 3 shows in detail the course of the tracheæ at the extreme base of the hind wing. In the fore wing the coalesced bases of *Cu* and *1st A* contain a single trachea, which soon divides, one branch following the *1st A*, the other branch immediately dividing again, both branches traversing *Cu*, but soon shriveling up. That portion of *Cu* between its separation from *1st A* and the posterior arculus (which is here transverse and contains no trachea) is evidently homologous with the oblique free portion of *Cu* in Micropterygidæ and Trichoptera. The tracheæ in the base of the hind wing (Fig. 3) show that the relations of *Cu* to the *1st A* are apparently the same as in the fore wing, but the separation takes place extremely close to the base, and the course of the veins is obscured by the tuberosities at the base of the wing. It will be observed that the vein containing a branched trachea, evidently the cubital trachea, is met very obliquely near the base of the wing by a vestige of what appears to be the posterior arculus. The evidence afforded by a study of pupal wings of *Prodoxus* (Fig. 6) supports the conclusions derived from a study of adult wings. The coalescence of *Cu* and *1st A*, the Z-shaped course of *Cu*, and the formation of the serial vein are sometimes shown with greater distinctness in the fore wing of *Adela bella* (Fig. 5), where these features of the venation are almost exactly as in *Mnemonica;* a similar condition is present

in the hind wing. The course of these veins is also the same in *Cyanauges cyanella*, as reference to Figure 4 will show; in this case the separation of *Cu* and *1st A* occurs almost at the base of the wing.

The obvious conclusion to be drawn from this series of examples is that in the course of evolution, the point of separation of *Cu* and *1st A* moves toward the base of the wing, and concomitant with this change, the oblique basal part of *Cu* becomes more and more oblique until by the time the point of separation has reached the base of the wing, the formerly oblique free basal part of *Cu* is in a line with the longitudinal part of *Cu*. There will thus be no evidence in the venation of this part of the wing in the more specialized Lepidoptera to indicate that it is derived from a venation like that of *Mnemonica*. What appears to be the posterior arculus is usually obsolescent (as indicated in the Figures by dotted lines), but vestiges of it sometimes traversed by a persistent trachea are present in many Lepidoptera belonging to widely separated groups, e. g., in Tineidæ (e. g., *Tineola*), Plutellidæ (e. g., *Pliniaca*), Eucleidæ (e. g., *Sisyrosea textula*), Tortricidæ, and possibly in other groups. The question whether this is really the posterior arculus or the base of M_4 is not discussed here. In the light of what has been shown to have taken place in more primitive forms, the configuration of veins in the base of the fore wing of the Noctuid, *Renia flavipunctalis* (Fig. 7), suggests the same course of evolution. The coalescence of the base of the first anal trachea with the cubital trachea, shown in the pupæ of some butterflies, and in some of the specialized moths (e. g., *Samia cecropia*), I am inclined to regard as a secondary connection, following the separation of *Cu* and *1st A* at the base.

The venation of the fore wing of the more generalized members of the Nepticulidæ is characterized by the basal coalescence of media and cubitus, a character unique in Lepidoptera, but whose origin can be explained by assuming that processes similar to what is known to occur in some Trichoptera have taken place. The cubital and medial tracheæ lie within the same vein cavity near the base (Fig. 8), the two separating at the point where media bends forward to join radius. This characteristic of the venation of the Nepticulidæ can be derived from an ancestral form in which cubitus followed

the course common to *Mnemonica* and *Rhyacophila*, if we assume an anastomosis of *M* and *Cu*, obliterating the posterior arculus (such as Comstock shows has taken place in a species of *Rhyacophila*) to have proceeded to the base of the wing. This view is strengthened by the course of the persistent cubital trachea in the fore wing of a specimen of *Nepticula platanella* (a comparatively generalized species of its genus) which follows the first anal vein at the base, bending obliquely toward media which it reaches at the point where media bends upward toward radius, then extending longitudinally along the usual course of cubitus. The venation of the hind wing shows an advance over that of the fore wing, even in the most generalized Nepticulidæ, in that media and radius coalesce for half their length; this condition, which is brought about by the crossing over of media to radius at the base has been attained in part of the genus *Nepticula* in the fore wing.

In the Hepialidæ the course of cubitus of the fore wing is the same as it is in the Micropterygidæ. In the hind wing *Cu* is free from *1st A* at its base; there is no evidence from pupal wings or adult forms to indicate how this condition may have been derived from one in which *Cu* follows the same course as in the fore wing.

The coalescence of the tips of two branches of the third anal vein with the tip of the second anal vein of the fore wing is a character common to both the more generalized Trichoptera and Micropterygidæ. The second branch of the third anal vein tends to disappear very early in phylogeny, although the third anal trachea is often forked in the pupa. Even in the most primitive Micropterygidæ, as *Sabatinca*, this coalescence of veins is shown in one species and not in the other. The second branch of the third anal vein is but faintly shown in *Epimartyria* (Fig. 1). In *Scoliaula* of the Nepticulidæ, there is a faint indication of a second branch of the third anal vein, represented merely by a broad slight thickening of the wing membrane, but neither it nor the first branch continue far enough to unite with the second anal vein. In Hepialidæ, the second branch of the third anal vein shows no tendency to unite with the first branch, but runs close to the margin of the wing. Among the Frenatæ, the condition of the branches of the third anal vein in *Prionoxystus* is similar to that in Hepialidæ.

In *Prionoxystus robiniæ*, the second branch of the third anal closely parallels the axillary furrow; the third branch follows the free margin of the posterior lobe. As shown later, the inner margin of the fore wing in this species clasps the costa of the hind wing. In other Frenatæ, I have found no indication of the presence of the second branch of the third anal vein. It is suggested as a plausible explanation of the atrophy of this vein that its disappearance is correlated with the loss of the holding function by this part of the wing.

The cross-vein between the first and second anal veins of the fore wing, which is present in Micropterygidæ and Trichoptera, is preserved in many of the primitive Frenatæ as well as in the Hepialidæ. It is shown distinctly in *Adela bella* (Fig. 5), and in *Prodoxus;* in a pupal wing of *Pronuba* this vein is as strong as the second anal. It is shown faintly in *Cyanauges cyanella*.

In the hind wing, the course of the second anal vein, which anastomoses with the first anal vein for a distance, is regarded by Comstock as a distinctly ordinal character, common to Micropterygidæ and Trichoptera (cf. The Wings of Insects, p. 310). The tracheation in the base of the hind wing of *Prodoxus* (Fig. 3), shows the same course of the second anal. The trachea of the second anal vein bends forward to the first anal vein, but almost immediately bends obliquely backward and after meeting the cross-vein between the second and third anal, extends in a longitudinal direction to the wing margin. The cross-vein is a much more distinct and well developed tubular vein than is the base of the second anal vein itself. The pupal tracheation of *Prodoxus* (Fig. 6) shows quite clearly the anastomosis of the first and second anal veins. In this instance the longitudinal cross-vein between the second and third anal veins is preceded by a trachea, which is apparently the first branch of the third anal itself. A similar condition is indicated by the course of these veins in *Cyanauges* and in *Adela;* in neither is verification possible through persistence of tracheæ. In *Adela* the base of the *2nd A* followed proximad, becomes indistinct before reaching the *1st A;* the cross-vein is quite distinct.

In Hepialidæ neither venation nor tracheation in the pupal wings (MacGillivray, '12), where there are three free anal tracheæ, indicates any such anastomosis.

Adela bella (Fig. 5) shows a branching of the third anal vein of the hind wing, similar to that in Micropterygidæ and Trichoptera.

It has just been shown that certain essential features of venation common to Micropterygidæ and Trichoptera and seemingly found in no other insects can be identified in more or less modified form in most of the more primitive Lepidoptera. In most cases the steps in this process of modification can be traced. The evidence is perhaps least satisfactory in the Hepialidæ, which would indicate their divergence from the other lepidopterous groups, a view borne out by other points of structure. It is apparent that these characteristic features of venation which the Micropterygidæ hold in common with the Trichoptera do not distinguish them from the rest of the Lepidoptera as sharply as might be inferred by a comparison of the Micropterygidæ with more specialized Lepidoptera only. The manner of specialization in the Nepticulidæ, with respect to the course of cubitus, is of especial value in determining the true phylogenetic relationship of the Micropterygidæ to the rest of the Lepidoptera. The course of modification in the more generalized Nepticulidæ, paralleling that sometimes occurring in Trichoptera, which is a divergence from the usual lepidopterous type, together with the possession of the fibula, undoubtedly indicates a common ancestry with Trichoptera, while certain other typically lepidopterous characters, such as the single spined frenulum of the male, the short tongue and six-jointed maxillary palpi characteristic of many primitive Frenatæ, obsolescence of the first anal vein of the fore wing, the reduction of radius of the hind wing in the same manner as it has taken place in the Frenatæ, place the Nepticulidæ with certainty in the Lepidoptera. This peculiar combination of characters in the Nepticulidæ, taken in connection with the undoubted specialization in venation, places them as the end group of a line of development divergent from that of the other Lepidoptera. Since these two *divergent* lines of development are both lepidopterous, the common ancestor must also be lepidopterous. It has just been shown, that the course of modification in venation in both lines of development can be traced back to Micropterygidæ, which therefore, on the basis of evidence derived from a study of venation, must be regarded as the common ancestor and is hence lepidopterous. To

remove the Micropterygidæ from the Lepidoptera, would necessitate the assumption that the Lepidoptera have originated twice or have been derived from a hypothetical lepidopterous ancestor so close to Micropterygidæ that it can not be separated from Micropteryidæ.

(*b*) *Mode of Insuring Synchronous Action of Fore and Hind Wings.*

The methods of holding the fore and hind wings together in flight show characteristics which are of value in a study of the phylogeny and relationships of the Trichoptera and Lepidoptera.

In the more generalized Trichoptera and in the most primitive groups of Lepidoptera, the posterior lobe of the fore wing has been modified to serve as an organ for holding the wings together, termed fibula or jugum, depending on mode of functioning. The fibula in the more generalized Trichoptera, such as Rhyacophila, and in certain of the Micropterygidæ, as *Mnemonica* in the subfamily Eriocraniinæ, acts by pressing downward over the base of the hind wing and clasping the anterior tuberosity of the hind wing. Tillyard ('18, '19) has described for certain genera of the two remaining subfamilies of the Micropterygidæ, the Mnesarchaeinæ and the Micropteryginæ, a different mode of functioning of the fibula. In these genera it is described as being bent under the fore wing and serving as a retinaculum for the series of costal spines of the hind wing.* My observations on *Epimartyria* in the subfamily Micropteryginæ tend to support this view.

The fibula in the female of the last specialized genera of Nepticulidæ (which find their nearest allies in characteristics of venation among the Hydroptilidæ in the Trichoptera) is identical in structure with the fibula in the more primitive Trichoptera and in the Micropterygidæ. In the Trichoptera the process of modification of the fibula has finally resulted in such a reduction in size and change in shape that the posterior lobe of the fore wing no longer bears any resemblance to a fibula and can not function to aid in holding the fore and hind wing together. In some forms, while not retaining the characteristic shape shown in the Rhyacophilidæ, the longitudinal free margin still shows the downward curve, thus indicating

* That these spines do not constitute a true frenulum and are not homologous with it, is shown in the pages following.

that it can still act by clasping the anterior tuberosity of the hind wing. The course of modification of shape in the posterior lobe of the fore wing in Nepticulidæ from a fibula in females of the more generalized genera can be traced through various changes until it becomes merely a narrow lobe whose free margin is continuous with the inner margin of the wing. Thus we find that while in the females of earlier genera the fibula has preserved its original structure and is apparently functional, in the males of these genera the posterior lobe is rather prominent but lacks the characteristic shape of the fibula as found in the Trichoptera and Micropterygidæ. In *Nepticula* the posterior lobe has lost all resemblance to the fibula; it is extremely narrowed and the axillary furrow is so indistinct as scarcely to separate it from the rest of the wing. This process, whose steps can be observed in this lepidopterous family, would seem to indicate the possibility that a similar process might have taken place in families of the Frenatæ, or in other words, that the Frenatæ have been evolved from ancestral forms in which a well developed fibula was present. There is some evidence to support this view. In *Prodoxus* the posterior lobe of the fore wing is more than usually prominent and is separated from the rest of the wing by a very distinct axillary furrow; it shows a strong tendency to fold under, thus seemingly retaining some of the function of the fibula, although it has lost its characteristic shape. In some Tineidæ, the posterior lobe of the fore wing bears some resemblance to a fibula, but it is not of a structure to be functional. In others of the Frenatæ where it can be distinguished, it is merely a narrow lobe whose free margin is continuous with the inner margin of the wing.

In the Hepialidæ the jugum, though homologous with the fibula, differs from it in shape and method of functioning. The difficulty in the way of deriving the Hepialidæ from ancestors with a fibula disappears if a process similar to that which is known to take place in the Nepticulidæ is postulated. The jugum, in accordance with this view, would be considered a development in another direction from the posterior lobe of the fore wing in a more or less reduced condition.

The fact that a fibula of identical structure, though showing some variation in function, is present in three different groups, two of which, the Micropterygidæ and Rhyacophilidæ, are primitive and approach one another closely in other char-

acteristics of the wings, indicates that it is a persistent primitive character handed down from the common ancestor. The Nepticulidæ show marked specialization and are the end of a line of development, having given rise to no other group. Though they are not apparently to be easily or directly derived from any existing group, the possession of this primitive character undoubtedly allies them more closely to the Micropterygidæ than to any other Lepidoptera, and also indicates trichopterous affinities. However, the possession by Micropterygidæ and Nepticulidæ of this character of primitive Trichoptera, while it indicates relationship to Trichoptera, need not be taken as a basis for regarding them as trichopterous insects, because as shown for Nepticulidæ, it has disappeared as a functional structure in males even of the less specialized genera, and its function has been taken over by a single-spined frenulum of a character typical of the males of the more specialized Lepidoptera. That is, the Nepticulidæ retain evidence of descent in the form of a fibula, but they have progressed far enough in the lepidopterous direction to have developed a distinctly lepidopterous structure. The undoubted relationship between the Nepticulidæ and the Micropterygidæ indicates that the Micropterygidæ are without doubt also lepidopterous, but being a more primitive group, have not traveled thus far toward the usual lepidopterous type in respect to mode of uniting the wings.

In Rhyacophilidæ and other groups of the Trichoptera, in Micropterygidæ, Nepticulidæ and many of the more primitive Frenatæ (Figs. 1, 2, 5, 4a, 8), there is a series of slightly curved stiff spines on the costa of the hind wing near the base, which lie against one of the anal veins of the fore wing, or catch into a similar series on the fore wing, or lie in the fold of the fibula, and aid in holding the wings together. These spines lie beyond the costal sclerite, not on it, as do the true frenulum spines. They are proximal to the humeral vein in forms where this vein is present. This series of spines is without doubt homologous in the various groups in which it occurs; it may be present in addition to other means of holding the wings together, or it may be the only method of insuring united action of fore and hind wings. It may be functional in females, while in the males of the same species its function has been taken over by some other structure. Thus in Nepticulidæ (Braun, '17),

these costal spines are functional in females, but in the male, where there is a single spined frenulum, they are rarely preserved with the same structure and function. In Nepticulidæ when functional, they are larger and stronger than in any other Lepidoptera (except perhaps *Opostega*); they are decidedly stronger than in the Micropterygidæ. The spines are present in several of the more primitive frenate lepidopterous groups, often in combination with other primitive characters, and sometimes persist in more specialized groups. In the females of many groups of Lepidoptera this is the only method of insuring the united action of the fore and hind wings. These spines are present in females in Prodoxidæ, Adelidæ and Incurvariidæ, together with a few weak and useless short spines in the position of the frenulum. Homologous structures much modified and without function of holding may be distinguished in the males in these families, together with a well developed single-spined frenulum. In many genera of *Lyonetiidæ* they persist particularly in the female where there is also a functional frenulum, and they may also be distinguished as definite structures in the male, different from the rest of the scale covering of the wing. It is questionable whether they are functional except in rare instances in this family.

The possession of the row of costal spines by many of the Trichoptera and by more primitive Lepidoptera indicates that it is a persistent primitive character, and as such indicates common descent of the two groups. The preservation of these spines in many frenate Lepidoptera is one of the few connecting links between them and the Micropterygidæ.

The series of costal hooks — the hamuli — which have developed in the more specialized families of Trichoptera as a means of locking the fore and hind wing together, is a specialization not found in the Lepidoptera.

The true frenulum spines are situated on the costal sclerite of the hind wing. Although structures homologous with a frenulum, consisting of several stiff spines on the costal sclerite of the hind wing are found in some of the more specialized Trichoptera, the frenulum in its specialized form, culminating in the single-spined frenulum with the well developed frenulum hook of the male, is a distinctly lepidopterous development. In most Trichoptera, in Micropterygidæ, in females of Nepticulidæ, in females of *Prodoxus*, *Adela*, etc. (Figs. 1, 2, 5, 4a, 8),

there are merely hairs or weak functionless setæ on the frenulum-bearing area; in these the function of holding the wings together is performed by some other structure. In the males of some of these, viz., Nepticulidæ, *Prodoxus*, *Adela*, etc., there is a strong single-spined frenulum, formed by the fusion of several spines, in some instances of as highly specialized a character as is found in any Lepidoptera. These forms furnish no evidence of the phylogenetic process of development of the frenulum or frenulum hook, but such evidence is furnished by the condition of the frenulum in some members of several groups which conserve other primitive characters. In Cossidæ and Megalopygidæ the frenulum is in a rudimentary condition, consisting of a bunch of spines, and in the females of many moths it consists of two or several spines. Of the process of transition from more primitive modes of holding the wings together to a functional frenulum, we have very little evidence. In this connection, the condition found in *Pronuba* is significant. In the female *Pronuba yuccasella* all except the two most proximal of the row of costal spines have become flattened and scale-like, and these two remaining spines are larger than any of the corresponding series found in *Prodoxus*, which is an allied, though more generalized genus. In addition in the female *Pronuba* the beginnings of a true frenulum are shown, consisting of a tuft of short, weak spines at the distal end of the costal sclerite in the same position as the frenulum of the male. There is also an inwardly projecting row of scales from the costa of the fore wing, apparently the beginning of a frenulum hook, which is present in the male. The female frenulum is not long enough to reach this row of scales, which is, however, easily reached by the two strong costal spines, which may thus *function* as a frenulum before the true frenulum has reached a sufficient size to be functional. These two spines are not present in the male *Pronuba*, which has a single-spined frenulum. In the Nepticulidæ there is no stage in the development of the frenulum intermediate between the minute functionless spines of the female, and the strong single-spined frenulum of the male. However, the fact that functional costal spines and frenulum are occasionally present at the same time, indicates that the costal spines retain their function up to the time that it is taken over by the frenulum. In the Cossid, *Prionoxystus robiniæ*, where the frenulum is rudimentary in both sexes, the

underside of the inner margin of the fore wing hooks against a strong ridge along the costa of the hind wing.

It is apparent then that a functional frenulum has originated independently in the Lepidoptera, and that it is not a primitive character derived from the ancestral lepidopterous stalk.

From the facts as above stated, it is equally apparent that the transition from more primitive modes of holding the wings together has taken place within the Lepidoptera, although in most cases the intermediate stages have not been preserved. That the frenulum originated independently several different times at least in the Lepidoptera is shown, first, by the fact that it appears in the Nepticulidæ, which is an end group not derived from or related to the frenate Lepidoptera; second, by the fact that it takes the place of costal spines in *Pronuba;* third, by the specialized condition of the frenulum in the males of certain groups, the females of which have a very rudimentary frenulum; fourth, by its rudimentary condition in other comparatively primitive groups, such as the Cossidæ, where there is no evidence of costal spines or similar holding structures, and the transition stage has been bridged by a very different means. It may have originated independently in other families, but we are without direct evidence to this effect; similarly it may have disappeared independently as is shown for example by its presence in *Euschemon* only, in the Hesperidæ.

The significant phylogenetic feature in the development of the frenulum is its appearance in the Nepticulidæ which is the end of a line of development, and which is related to Micropterygidæ and must be regarded as derived from them, and its independent appearance in the group usually known as the Frenatæ. No similar course of development is to be witnessed in the Trichoptera. The evidence for phylogeny derived from the frenulum in my view points unmistakably to the conclusion that the branch of the ancestral stem which produced Micropterygidæ and Nepticulidæ must also have given rise to the rest of the Lepidoptera and hence all should be included in one order.

(*c*) *Distribution of Fixed Hairs.*

A character, which when present, may without doubt be regarded as a persistent primitive character is the presence of the fixed hairs upon the wing surface. These are characteristic

of the Trichoptera, the Micropterygidæ and certain other of the more primitive families of the Lepidoptera, Nepticulidæ, Hepialidæ, Incurvariidæ, etc., where they are distributed over the entire wing surface, but even in these most plentiful on the underside of the fore wing near the dorsal margin. In many Lyonetiidæ, e. g., *Hieroxestis*, *Oinophila*, *Coptodisca*, besides the fixed hairs on the underside near the inner margin, there is a patch in the middle of the fore wing near the base; in *Tischeria* and *Opostega*, there are additional scattered fixed hairs on the wing surface. In other groups the fixed hairs are confined to the under side of the fore wing near the base of the dorsal margin, with the rare presence of such hairs on other parts of the wing, e. g., in *Tineola*. The very fact that the fixed hairs are most numerous in the most primitive groups, tending to become scattered and later confined to definite areas of the wing, and finally persisting only in a limited area on the underside of the fore wing, where they may function to a slight degree in holding the wings together in flight, shows that while taken in connection with other characters, their presence may indicate a comparatively primitive condition of the forms possessing them, the character is not one upon which a taxonomic division can be made.

III. Summary and Conclusions.

The discussion of wing structure in Lepidoptera has dealt chiefly with those characters which have been handed down from the common ancestor of both Lepidoptera and Trichoptera, and which have been preserved without modification in the most primitive Lepidoptera, but which have undergone more or less far-reaching modification in all other groups of Lepidoptera. In many instances the steps in the process of modification have been traced, and it has been possible to identify these characters in their modified form in many of the more primitive groups of frenate Lepidoptera. These changes in structure have sometimes been correlated with changes in function of certain parts of the wing or with the taking over of a particular function by a different organ.

The conclusion reached from a study of certain features of venation is that the Micropterygidæ are not as sharply separated from the rest of the Lepidoptera as might be inferred from a

comparison made only with more specialized groups of Lepidoptera. The modifications which are shown in the more primitive groups of frenate Lepidoptera have their beginnings in the Micropterygidæ themselves. In addition we have the evidence given by the Nepticulidæ, which combine in one group, certain characters found in the Frenatæ, with characters belonging to the Micropterygidæ and in the manner of specialization of certain characters of venation diverge from all other Lepidoptera, paralleling what occurs in some Trichoptera. The existence of these *divergent* groups, the Frenatæ and the Nepticulidæ, both of which are derived from Micropterygidæ, is conclusive evidence of the lepidopterous character of their common ancestor, the Micropterygidæ, even if we do not take into consideration such features of the Micropterygidæ as the character of the mouth-parts and the scale covering of the wings, which unmistakably stamp them as lepidopterous.

The conclusion drawn from a study of the various modes of holding the wings together in flight in the Lepidoptera, is that in the more primitive groups of Lepidoptera, including the Micropterygidæ, certain trichopterous structures are retained and are functional, but in higher groups are modified or disappear and their function is taken over by other wing structures, chief of which is the frenulum. The frenulum in its specialized form is shown to have had its origin in the Lepidoptera and to have developed independently in several widely separated groups.

Certain general phylogenetic and taxonomic conclusions follow from these studies. The Micropterygidæ are close to the common ancestor of both Lepidoptera and Trichoptera, but are true Lepidoptera. From them the remaining Lepidoptera have been derived, not from a single line of descent, but from several divergent lines, one of which is represented by the Nepticulidæ alone; a second line by the Hepialidæ, with the Prototheoridæ apparently forming a link between it and the Micropterygidæ, and to which the Cossidæ show some degree of relationship; a third much branched line includes the frenate Lepidoptera, of which some members such as the Prodoxidæ, Incurvariidæ, etc., conserve some of the trichopterous characters of their ancestry and must therefore be regarded as the most primitive of the Frenatæ.

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EXPLANATION OF PLATE XXIX.

Fig. 1. Wings of *Epimartyria auricrinella.*
Fig. 2. Wings of *Prodoxus quinquepunctellus*, female.
Fig. 3. Base of hind wing of *Prodoxus quinquepunctellus*, female.
Fig. 4. Wings of *Cyanauges cyanella*, male; 4a, base of costa of hind wing of female.
Fig. 5. Wings of *Adela bella*, female.
Fig. 6. Tracheation of pupal wings of *Prodoxus quinquepunctellus.*
Fig. 7. Base of fore wing of *Renia flavipunctalis.*
Fig. 8. Wings of *Ectoedemia heinrichi*, female.