

A STUDY IN BUTTERFLY WING-VENATION, WITH SPECIAL REGARD TO THE RADIAL VEIN OF THE FRONT WING

By THOMAS J. HEADLEE

After making wide studies of pupal and adult wings in nearly all orders of insects, Comstock and Needham ('98)¹ constructed an hypothetical type of wing venation, which they believed closely to represent, in number and branching of the veins, the condition that existed in the ancestors of the present winged insects. Later ('04), Comstock² modified this type by the addition of three typical cross veins (text fig. 30).

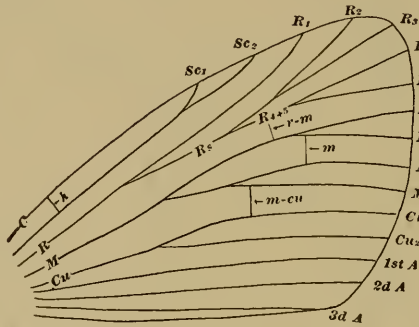


FIG. 30.—Hypothetical type of primitive insect wing.

In passing from this to the lepidopterous type, the third anal vein of the fore wing becomes two-branched, and the second anal vein of the hind wing two-rooted (text figs. 31, 32). Except in the anal area where there has been a great reduction, such *Jugatae* as *Hepialus* and *Sthenopsis* well represent this type (pl. LX, figs. 1-4).

However, by far the larger number of Lepidoptera belong to the *Frenatae* and exhibit a much greater modification of wing veins. In passing from the generalized lepidopterous to the *frenate* type, the humeral cross-vein disappears, subcosta of both wings is reduced to an unbranched vein, media of both wings reduced to three branches,

¹ J. H. Comstock and J. G. Needham, *The Wings of Insects*, *Amer. Nat.*, xxxii and xxxiii, 1898 and 1899.

² J. H. Comstock, *How to Know the Butterflies*, p. 9, 1904.

and in the hind wing costa has become a mere vestige in the humeral edge of the wing, a frenulum is developed on the humeral angle, radius reduced to two branches, and radius-one coalesced with subcosta from distal end almost to base (text figs. 33, 34). This type is illustrated by *Castnia cochrus* (pl. LX, figs. 5, 6).

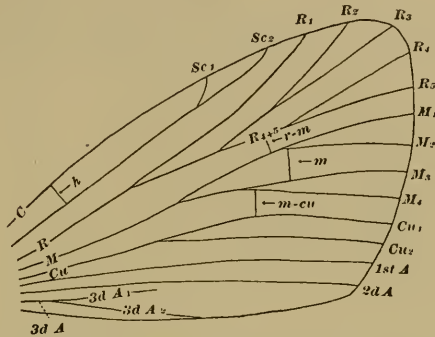


FIG. 31.—Hypothetical type of primitive lepidopterous fore wing.

With the exception of the two-rooted condition of the second anal vein of the hind wing, all these modifications have been recognized and discussed by previous workers, so I shall pass them without further discussion. Inasmuch as this two-rooted condition appears in some of the most generalized Lepidoptera and in widely

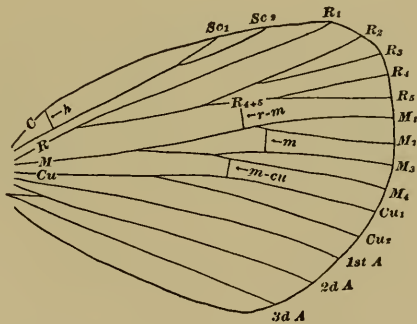


FIG. 32.—Hypothetical type of primitive lepidopterous hind wing.

separated forms, such as *Micropteryx*, *Prionoxystus robiniae*, *Phassus triangularis*, and *Euschemon rafflesiae*, it should be figured in the lepidopterous hypothetical type (text figs. 32, 34, pl. LXI, figs. 7 to 10).

Extended study of pupal and adult wings has convinced me that,

while the frenate type of hind wings will serve, unmodified, as typical of both heterocerous and rhopalocerous hind wings, the frenate type of fore wing will by no means serve equally well as typical of these fore wings. While the latter will serve as a type of the

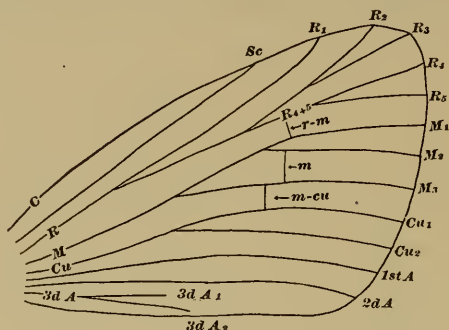


FIG. 33.—Hypothetical type of primitive frenate fore wing.

frenate heterocerous fore wing, the rhopalocerous type shows a different condition of radius (text fig. 35).

Inasmuch as the wide occurrence and the significance of this modification of the rhopalocerous radius has been heretofore overlooked, I will discuss it in detail.

In the hypothetical type of insect wing, radius is primarily two-branched, forming radius-one and the radial sector. The latter soon

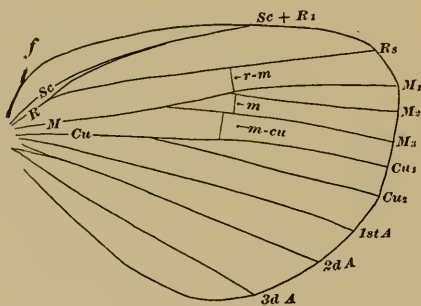


FIG. 34.—Hypothetical type of primitive frenate hind wing.

divides, giving rise to radius-two-plus-three and radius-four-plus-five. Each of these again divides into two branches, radius-two-plus-three into radius-two and radius-three; radius-four-plus-five into radius-four and radius-five. Thus the vein ultimately becomes five branched.

My own studies have convinced me that this primitive type of radius prevails among the most generalized lepidoptera such as *Hepialus*, *Sthenopsis*, and *Castnia cochrus*. Spuler also evidently considered this type the most primitive in the Lepidoptera, for he figured this exact condition in his "Schema des Vorderflügelgeäders der Schmetterlinge"¹ (pl. LX, figs. 1-5 and 11).

This, then, being the prevailing condition of radius not only in the most generalized lepidopterous wings but also in generalized insect

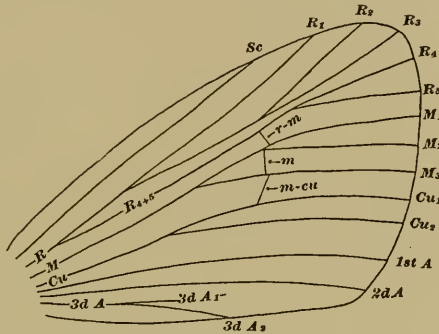


FIG. 35.—Hypothetical type of primitive rhopaloceros fore wing.

wings generally, as was shown by Comstock and Needham, may safely be laid down as the primitive lepidopterous radius from which the present types have been developed. Usually the modifications take the form of a coalescence between the radial branches, or of a more or less complete atrophy of individual branches. In fact, these are the means by which the heterocerous radius has been modified. The rhopaloceros radius, on the other hand, shows not only the effects of such modifications but of a splitting back of R_{4+5} until it finally comes to arise near the base of the main stem of radius (text fig. 35). The traces of the last appear in the adult wing of *Anosia plexippus* in the form of two spurs and a connecting line. One of the spurs is very short and projects from the base of radius into the discal cell and toward the outer edge of the wing, the other projects from the base of M_1 into the discal cell and toward the base of the wing, while the line connects the two spurs (plate fig. 12). Although these traces are of themselves suggestive, they are not convincing proof of such a modification of radius. The tracheation of the pupal wing, however, clearly explains and supplements the evidence furnished by these remnants. Trachea R_{4+5} is found to follow

¹ A. Spuler, Zur Phylogenie und Ontogenie des Flügelgeäders der Schmetterlinge, *Zeitschr. wiss. Zool.*, LIII, 4, 1892, pp. 597-646.

exactly the line which, in the adult wing, will be occupied by the structures just described (pl. LIX, 1). These spurs surely represent a once well-developed vein which in the course of phylogeny has almost disappeared. As might be expected from the fact that they are vestiges of a disappearing structure, these traces vary in degree of preservation from a strong well-marked condition to total absence. It is comparatively rare to find the line and both spurs well preserved in the same wing; usually one or more of these vestiges has been lost. The spur at the outer end of the cell is not always on M_1 but in many cases rests on radius, as in *Semnopsyche diana* (plate fig. 13). It is not always an easy matter to see these traces, even in cleared and mounted wings where they are present, but in photographs, where all structures are magnified, their presence can readily be detected. There are, however, numerous examples in which such vestiges are visible in the unbleached and unmounted wing, as in certain species of the larger *Papilios* (pl. LIX, 2). The variation in the position of the spur lying nearer the outer end of the discal cell is significant of different courses of phylogenetic development. These I shall attempt to trace in the following paragraphs.

In many wings, such as those of *Anosia plexippus* and *Apostraphia charithonia*, this spur is located on the base of M_1 ; in others, of which *Semnopsyche diana* is typical, it occurs on radius just before the end of the discal cell; and in still other cases, such as *Diathria clymena*, it lies on radius proximad of the origin of R_1 (pls. LX, LXI, figs. 12-15). All stages from the condition in *Anosia* to that in *Diathria* have been found.

The position of the spur on the base of M_1 is due to a complete coalescence of R_{4+5} with the radio-medial cross-vein and, following that, a short coalescence with M_1 . While this process has resulted in the real obliteration of the radio-medial cross-vein, it has produced an apparent cross-vein between M_1 and R ; for, when the basal part of R_{4+5} has atrophied, nothing but a more or less well-marked stump is left on M_1 to explain that this apparent cross-vein is none other than the stem R_{4+5} passing over to coalesce for a distance with R before reaching the outer edge of the wing. This apparent cross-vein differs in direction from the real cross-vein. The former extends obliquely from M_1 toward the apex of the wing, while the latter extends obliquely from R toward the outer hind corner (plate figs. 14 and 15). The first type is almost characteristic of the Neotropidæ, Danaidæ, Heliconidæ, and Libytheidæ, and the second occurs very generally in the Nymphalidæ, Satyridæ, Morphidæ, Brassolidæ, and Acraeidæ.

The variation in the position of this spur nearer the outer end of the discal cell is due, when it lies on radius, to the distance to which the coalescence between R_{4+5} and R has proceeded toward the base of the wing. It may have continued to a point just proximad of the discal cell apex, as in *Semnopsyche diana*, or it may have continued until, as shown in *Diathria clymena*, R_{4+5} both arises from and again fuses with radius before R_1 arises (pl. LXI, figs. 13 to 15).

In all these cases, however, that part of R_{4+5} within the limits of the discal cell and not coalesced is always more or less completely atrophied. In order to understand how this has come about, it is necessary to sketch some of what I believe to be the phylogenetic history of this vein.

Primitively R_{4+5} was unconnected with radius except at point of origin. Later a connection between it and R was established at or near the apex of the present discal cell. This connection, which took in some cases the form of a short cross-vein and in others the form of a coalescence, must have preceded any weakening of the former vein because, so long as R_{4+5} was the sole air passage to and brace-rod of the veins R_4 and R_5 , natural selection would tend to preserve it, but when this connection became established that part of R_{4+5} between the origin and the connection became not only useless but, through its weight and the energy consumed in forming it, a positive handicap to the species possessing it. Tendencies toward atrophy of this part were seized upon by natural selection and in the forms that we know, it has everywhere disappeared as a distinct vein, leaving only more or less well-preserved vestiges.

From the fact that this modification of radius, the variation and loss of which we have just seen, seems to have come about through a splitting back of the vein in question, I shall refer to it as the split-back condition of R_{4+5} . It is also to be noted that the places at which the other branches of radius originate have moved, if at all, toward the outer edge of the wing.

Spuler found this condition of radius in the pupal wings of *Vanessa io* and *Papilio machaon* and gave good figures of pupal and adult wings showing it. He, however, considered the state of radius in *Dasychira pudibunda*, in which trachea R_{4+5} arises from trachea R proximad of the origin of R_1 , as comparable to although less developed than, that in *Vanessa* and *Papilio* (pl. LXI, fig. 16). This is not the case, for the actual point of origin of R_{4+5} is not greatly changed, as may be seen by a comparison of it with the forking of media. This deceptive appearance is due to the coalescence of R_1 ,

with R_5 and R_{2+3} , as is also a similar appearance in the adult wing of *Tascina orientalis*. This discovery of a split-back condition of R_{4+5} in *Papilio* and *Vanessa* has passed unnoticed by later workers.

Although these vestiges in three forms of Rhopalocera (*Anosia*, *Papilio*, and *Vanessa*) should certainly be interpreted as evidence of a split-back condition of the vein R_{4+5} , it was necessary that pupal conditions in other groups should be investigated before the same interpretation could be applied to similar structures in them. Accordingly I have removed, mounted, and photographed pupal wings of *Epargyreus tityrus*, *Anosia plexippus*, *Papilio polyxenes*, *Euvanessa antiopa*, *Basilarchia archippus*, *Vanessa cardui*, *Pieris rapæ*, and *Feniseca tarquinius* (pls. LXI, LXII, figs. 17, 21, 25, 27, 29, and LIX, fig. 1). In the first six, radius showed very clearly this split-back condition but, although all stages from the mature caterpillar to the adult butterfly were examined, the last two showed a four-branched radial trachea in which there was no evidence of any such modification. The choice of *Pieris rapæ* as a representative of the Pieridæ was unfortunate, for all traces of this splitting back of R_{4+5} have disappeared from both pupal and adult wings, while the adult wings of *Eurymys philodice* and *Anthocharis sara* show these traces very well preserved and it is therefore very probable that, had their pupæ been examined, the split-back condition of R_{4+5} would have been found (pl. LXII, figs. 31 and 32). On the other hand, *Feniseca* was probably as good a type as the North American Lycænidæ could furnish, for the vein reduction has proceeded to such an extent in this family that very few of its members retain any traces of this modification. The forms in my possession which do retain such traces come from South America and southern Asia (pl. LXIII, fig. 33).

The wide occurrence of these vestiges, which are clearly remnants of a split-back condition of the vein R_{4+5} , renders entirely justifiable the interpretation of similar structures in related forms as homologous and signifying the same condition. These vestiges occur in all families and in the following examples they are especially well marked: *Epargyreus tityrus* of the Hesperidæ; *Papilio polyxenes* of the Papilionidæ; *Parnassius smitheus* of the Parnassidæ; *Hypatus bachmani* of the Libytheidæ; *Anosia plexippus* of the Danaidæ; *Leucothyris quinatina* of the Neotropidæ; *Apostraphia charithonia* of the Heliconidæ; *Semnopsyche diana* and *Euphydryas phaeton* of the Nymphalidæ; *Catoblepia* sp. of the Brassolidæ; *Morpho* sp. of the Morphidæ; *Erebia tyndarus* of the Satyridæ; *Anthocharis sara* of the Pieridæ; *Arhopala hercules* of the Lycænidæ (pls. LX-LXIII, figs. 18, 22, 34, 35, 12, 38, 14, 13, 37, 36, 39, 40, 32 and 33).

I have cited only a few of the examples available and, while they show how widely this modification is scattered through the groups, they show nothing of its prevalence among the members of the individual families, and consequently nothing very conclusive as to its history and significance. In order to get light on this point I carefully examined the mounted and photographed wings of 171 species, representing 158 genera and 16 families of Rhopalocera. These wings were taken from specimens representing all the life zones of the world, a majority being secured from North, Central, and South America. This latter fact does not impair the universal nature of the evidence for South America alone, according to Staudinger and Schatz ('85),¹ possesses 272 genera represented by 4,500 species, or about one-half of all the butterflies then known. All my specimens of the following families show traces of a split-back condition of R_{4+5} : four genera of the Papilionidæ; one genus of the Parnassidæ; one genus of the Danaidæ; fourteen genera of the Neotropidæ; three genera of the Heliconidæ; one genus of the Libytheidæ; two genera of the Brassolidæ; one genus of the Morphidæ. In the following families the relative number which show distinct traces of this modification is indicated by per cent: 89 per cent. for forty-one genera of the Nymphalidæ; 80 per cent. of fifteen genera of the Satyridæ; 76 per cent. of eight genera of the Hesperidæ; 70 per cent. of twenty genera of the Pieridæ; 50 per cent. of one genus, represented by two species, of the Acraeidæ; 14 per cent. of seven genera of the Erycinidæ; 7 per cent. of twenty-seven genera of the Lycænidæ. Thus in eight families all specimens and in five 50 per cent. or more show traces of this modification of radius, while in only two does the per cent. fall below fifty. These facts serve to show that this modification of radius is exceedingly prevalent and, to the student of rhopaloceros wings, also that, in general, it prevails most completely in those wings which have experienced the least reduction of other veins and are, in fact, the most generalized.

The wide distribution of this modification of radius and the fact that it is best preserved in generalized wings, can best be accounted for by the supposition that radius of the progenitors of the present butterflies was characterized by a split-back condition of R_{4+5} . This character has arisen, reached its maximum development, and is now reduced to mere vestiges, even these having almost disappeared in some families.

¹O. Staudinger and E. Schatz, *Exotische Schmetterlinge*, II Theil, 1885, p. 28.

Having seen the prevalence and primitive nature of this character in the Rhopalocera, the question arises as to what extent radius is thus modified in the Heterocera. To answer this I removed, photographed, and studied the pupal wings of the following moths, without, however, finding any trace of a split-back condition of R_{4+5} : *Carpocapsa pomonella* of the Tortricina, *Datana* sp. of the Notodontidæ, an undetermined species of the Geometrina, *Plusia brassicæ* of the Noctuidæ, *Alypia octomaculata* of the Agaristidæ, *Pyrrharctia isabella* of the Arctiidæ, *Phlegethontius celeus* and *Ampelophaga myron* of the Sphingidæ, *Samia cecropia*, *Telega polyphemus*, and *Callosamia promethea*, of the Saturniina, *Clisiocampa americana* of the Lasiocampidæ. Spuler has figured the pupal wings of *Mamestra brassicæ*, *Harpya vinula*, and *Smerinthus ocellata*, and none show any traces of this modification. Finding that tracheation showed no evidence of a split-back condition of R_{4+5} , I turned to the adult wings and carefully examined for such traces as were so abundant among the butterflies, 287 cleared and mounted wings, representing 216 genera and 35 families drawn principally from North America, but including such generalized forms as *Sthenopsis* and *Hepialus*, and found no trustworthy evidence of any such modification. It is difficult to believe that were such vestiges at all prevalent, they would have been overlooked.

The great prevalence in Rhopalocera and the total absence in Heterocera of this split-back condition of R_{4+5} affords a striking and genetic difference between butterflies and moths. It adds a new proof to that already existing for the accepted belief that the butterfly groups are more closely related to one another than to any other living Lepidoptera.

While butterfly wings conclusively show that a split-back condition of R_{4+5} was certainly characteristic of the rhopalocerous progenitors, moth wings hint at no such condition of radius in the heterocerous progenitors. In fact, everything shows conclusively that radius was of the type represented in Spuler's lepidopterous hypothetical type, and Comstock and Needham's hypothetical type for insects. Here, then, is the point of divergence between the heterocerous and rhopalocerous stems. This separation clearly did not occur until after the Lepidoptera had divided into Jugatæ and Frenatæ, for the reduction of radius of the hind wing to a two-branched condition, and the possession of a frenulum by the male of *Euschemon rafflesia*, shows that the butterflies clearly belong to the Frenatæ.

We must now make use of the anal area. Inasmuch as the anal veins in the front wings of some Rhopalocera, such as *Anosia* (plate figs. 12 and 20), have been reduced more rapidly than those of the hind wings, while in other forms, such as *Papilio* (plate figs. 22 and 24), the anal veins of the hind wings have been reduced more rapidly than those of the front wings, the rhopalocerous progenitor must have had the same number of anal veins in each wing. Likewise, inasmuch as the frenate Heterocera exhibit a similar variation, the butterfly stem must have separated from the frenate stem while the number of anal veins in each wing was the same.

The Rhopalocera, according to this view, separated from the other Frenatæ while the number of anal veins in each wing was the same and when R_{4+5} became split-back to the base of radius.

In the preceding discussion I have tried to make the following points:

1. Radius of the rhopalocerous front wing exhibits a split-back condition of radius-four-plus-five.
2. This modification, now almost lost in the adult wings, characterized the wings of the primitive Rhopalocera.
3. Radius of the heterocerous front wing exhibits no traces of such a modification, and such a modification is therefore not characteristic of the primitive frenate Heterocera.
4. This modification of radius is a phylogenetic difference between butterflies and moths and is one of the characters on which the two groups diverge.
5. This divergence took place after the Frenatæ had separated from the Jugatæ, while the number of anal veins in the front and in the hind wings was the same, and when radius-four-plus-five became split-back to the base of radius.

In conclusion, I wish to acknowledge my indebtedness to Dr. A. D. MacGillivray whose helpful suggestions and criticisms have been invaluable, and to Prof. J. H. Comstock whose criticism and willingness to furnish material have made the execution of this work possible.

LIST OF ABBREVIATIONS

C—Costal vein or trachea.

Sc—Subcostal vein or trachea.

*Sc*₁ and *Sc*₂—First and second branches of subcosta.

R—Radial vein or trachea.

*R*₁, *R*₂, *R*₃, *R*₄, and *R*₅—First, second, third, fourth, and fifth branches of radius.

M—Medial vein or trachea.

*M*₁, *M*₂, *M*₃, and *M*₄—First, second, third, and fourth branches of media.

Cu—Cubital vein or trachea.

*Cu*₁ and *Cu*₂—First and second branches of cubitus.

1st *A*—First anal vein or trachea.

2d *A*—Second anal vein or trachea.

3d *A*—Third anal vein or trachea.

3d *A*₁ and 3d *A*₂—First and second branches of third anal.

f—Frenulum.

H—Humeral vein or trachea.

h—Humeral cross-vein.

r-m—Radio-medial cross-vein or -trachea.

m—Medial cross-vein.

m-cu—Medio-cubital cross-vein or -trachea.

EXPLANATION OF PLATES

PLATE LIX

- FIG. 1. Photograph of pupal fore wing of *Anosia plexippus*.
 2. Photograph of the under side of the unbleached wings of *Papilio* sp. In this form the proximal ends of the well-preserved veins bear white scales on the under side of the wings, which thus bring them into strong contrast with the darker scaled wing membrane. The vestiges of those parts of R_{4+5} and M which cross the discal cell are also covered with these white scales and are thereby made very conspicuous.

PLATE LX

- FIG. 1. Front wing of *Hepialus* sp.
 2. Hind wing of *Hepialus* sp.
 3. Front wing of *Sthenopsis* sp.
 4. Hind wing of *Sthenopsis* sp.
 5. Front wing of *Castnia cochrus* Fabricius.
 6. Hind wing of *Castnia cochrus* Fabricius.
 7. Hind wing of *Micropteryx* sp. (After Comstock.)
 8. Hind wing of *Prionoxystus robinia* Peck. (After Comstock.)
 9. Hind wing of *Phassus triangularis* H. Edwards.
 10. Hind wing of *Euschemon rafflesia* Macl.
 11. Diagram of the venation of the fore wing. (In every respect save that of naming the veins this is a copy of Spuler's figure.)
 12. Front wing of *Anosia plexippus* Linnæus.

PLATE LXI

- FIG. 13. Front wing of *Semnopsyche diana* Cramer.
 14. Front wing of *Apostraphia charithonia* Linn.
 15. Front wing of *Diethria clymena* Cramer.
 16. Front pupal wing of *Dasychira pudibunda* Linn. (In every respect save that of naming the veins this is a copy of Spuler's figure.)
 17. Front pupal wing of *Epargyreus tityrus* Fabricius.
 18. Front wing of *Epargyreus tityrus*.
 19. Hind pupal wing of *Anosia plexippus* Linn.
 20. Hind wing of *Anosia plexippus* Linn.
 21. Front pupal wing of *Papilio polyxenes* Fabr.
 22. Front wing of *Papilio polyxenes* Fabr.

PLATE LXII

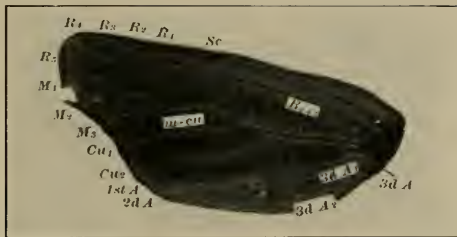
- FIG. 23. Hind pupal wing of *Papilio polyxenes* Fabr.
 24. Hind wing of *Papilio polyxenes* Fabr.

25. Front pupal wing of *Euvanessa antiopa* Linn.
26. Front wing of *Euvanessa antiopa* Linn.
27. Front pupal wing of *Basilarchia archippus* Cram. (This wing was injured in the outer margin and anal region.)
28. Front wing of *Basilarchia archippus* Cram.
29. Front pupal wing of *Vanessa cardui* Linn.
30. Front wing of *Vanessa atalanta* Linn.
31. Front wing of *Eurymus philodice* Godart.
32. Front wing of *Anthocharis sara* Boisduval.

PLATE LXIII

- FIG. 33. Front wing of *Arhopala hercules* Hewitson.
34. Front wing of *Parnassius smitheus* Doubleday and Hewitson.
35. Front wing of *Hypatus bachmanni* Kirtland.
36. Front wing of *Catoblepia* sp.
37. Front wing of *Euphydryas phaeton* Drury.
38. Front wing of *Leucothyris quinatina* Felder.
39. Front wing of *Morpho* sp.
40. Front wing of *Erebia tyndarus* Esper.

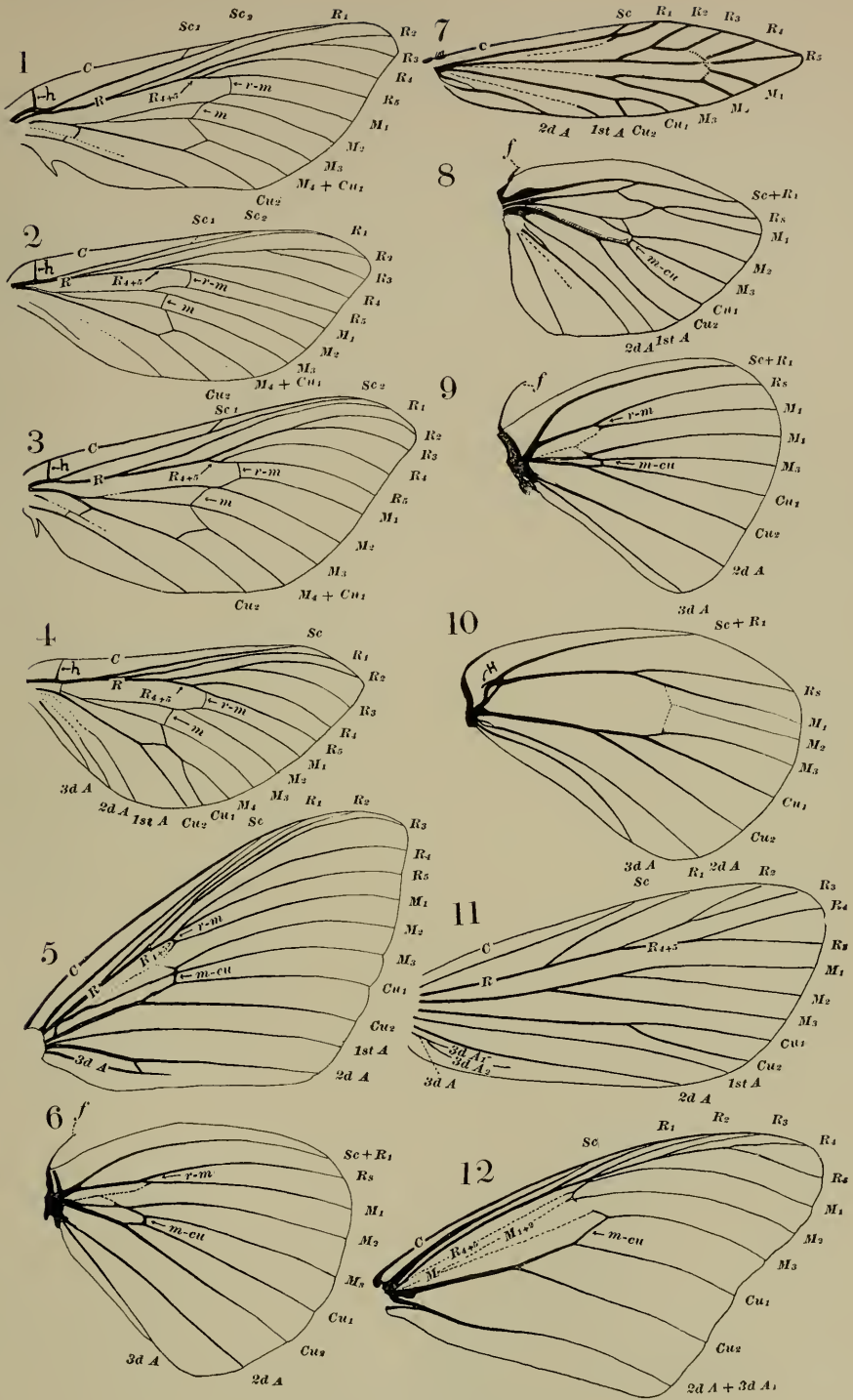
NOTE:—The wings figured in these plates are reproductions of the venation shown in the photographs. The image was printed on blue-print paper, the veins and outline were carefully inked in, and the blue removed by soaking in a saturated solution of potassium oxalate. Some of the pupal wings were torn in removing from the body and these were inked just as printed.



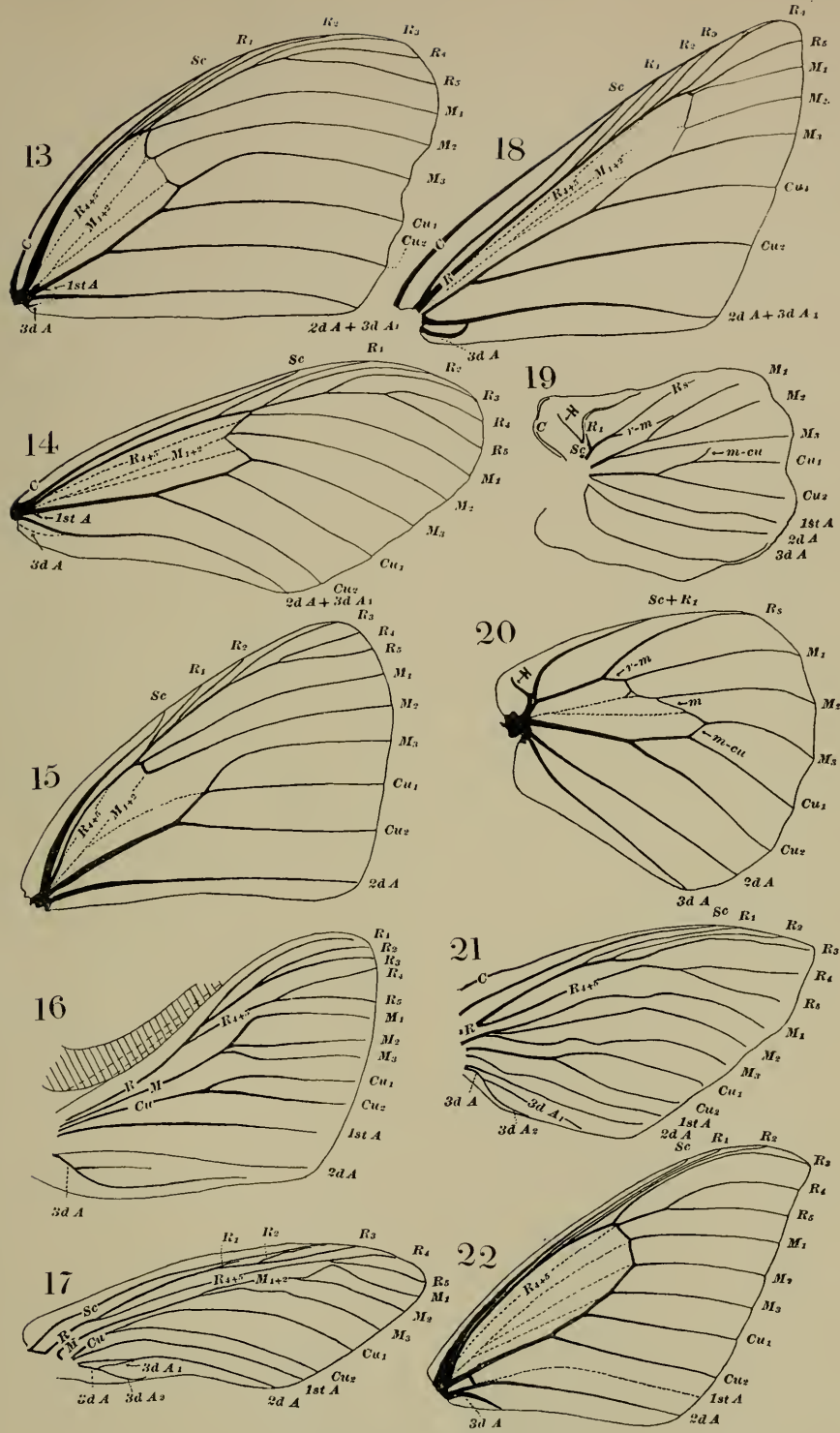
1. PUPAL FORE WING OF ANOSIA PLEXIPPUS.



UNDER SIDE OF UNBLEACHED WINGS OF PAPILIO SP.

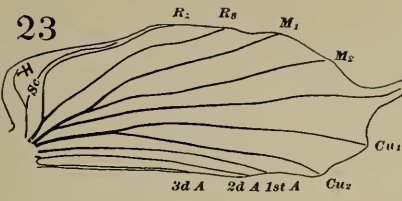


BUTTERFLY WING-VENATION.

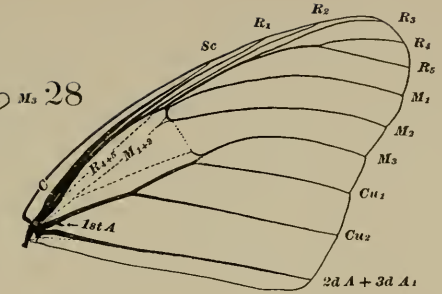


BUTTERFLY WING-VENATION.

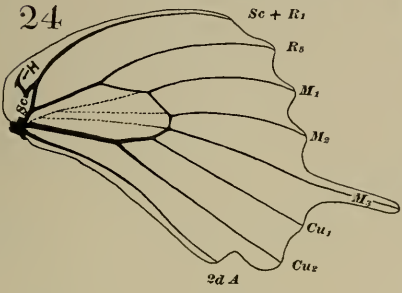
23



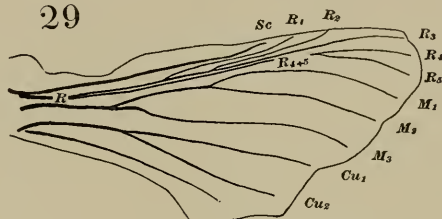
28



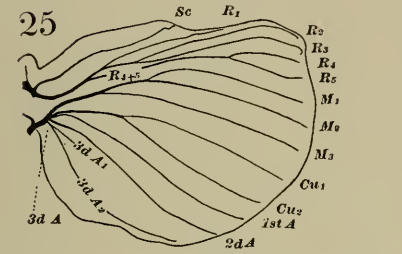
24



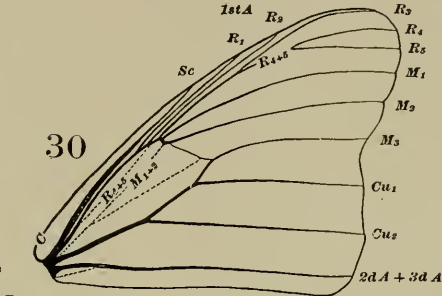
29



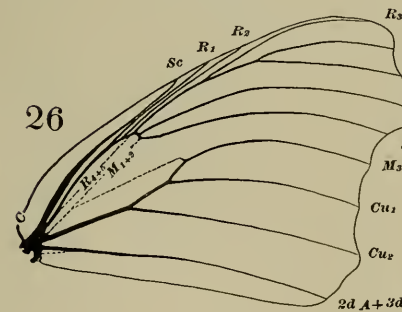
25



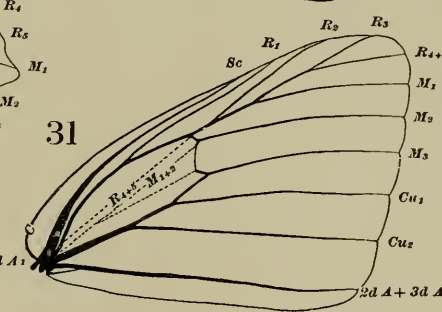
30



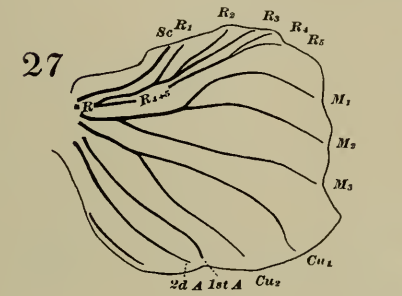
26



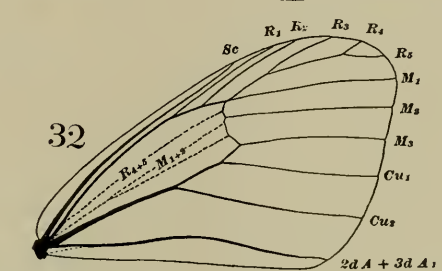
31

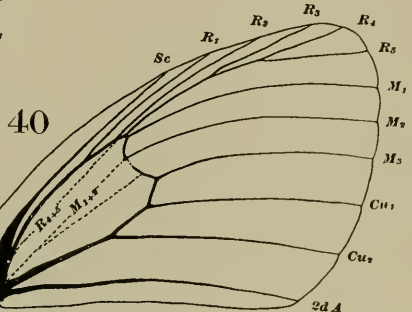
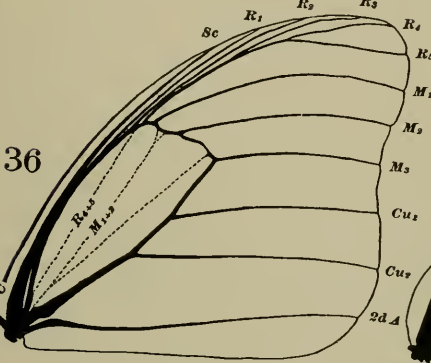
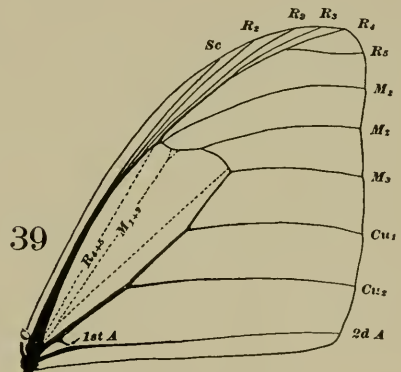
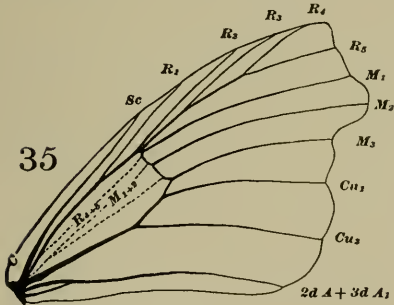
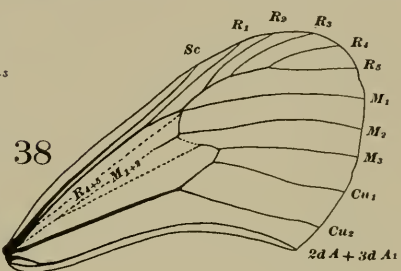
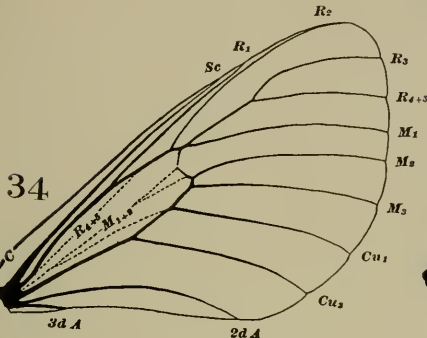
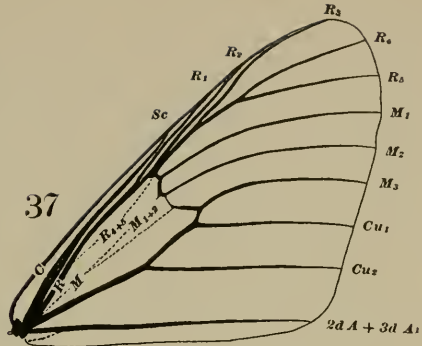
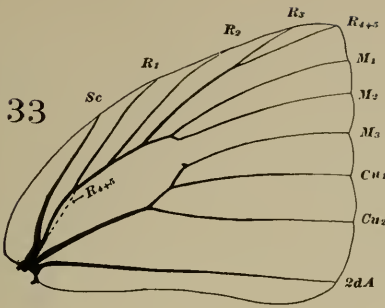


27



32





BUTTERFLY WING-VENATION.

