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HOMOLOGIES IN THE WING-VEINS OF MAY-FLIES.

ANNA HAVEN MORGAN.*

The following paper is an attempt to homologize the wing-veins of May-flies by a study of the tracheæ which precede them in the nymphal wing-pad.

The venation of May-flies has been many times discussed but only one work, that of the well known "Wings of Insects" by Comstock and Needham, has approached it from the standpoint of tracheation. This work suggested the present study.

At the outset I wish to express my indebtedness to Professor J. H. Comstock and Professor J. G. Needham for their many valuable criticisms. The work was done under the supervision of Professor A. D. MacGillivray, and while he disagrees with some of the interpretations herewith presented his constant interest and advice have made this study possible.

Material and Methods.

The genera with which this study deals are Epeorus, Iron, Ameletus, Ephemera, Blasturus, Hexagenia, Polymitarcys, Ephemerella, Siphlurus, Callibætis, Chirotonetes, Heptagenia, Leptophlebia, Choroterpes, and Cænis. Nymphs belonging to these fifteen genera were collected through the months from April to July inclusive, in the streams about Ithaca. They present as wide a range of variation as it was possible to obtain. The nymphs selected were those nearly matured whose wing-pads bore traces of venation easily seen with a hand lens. These were supplemented by younger nymphs showing tracheation only. Recently molted nymphs were used, since the wings of these lie flat upon the slide and both tracheation and venation show with great clearness. The method of preparation was that of the simple glycerine jelly mount. Nymphs were kept at hand in a dish of water. The wing-pad of one of the nymphs

*Entomological Laboratory, Cornell University.

was quickly severed with a razor together with a portion of the thorax, in order to preserve the connection between the wing and body trachea. The wing was then placed upon a moistened slide and a cover glass bearing a little melted glycerine jelly was laid over it. The preparation was immediately cooled upon a slab of iron. It was examined as soon as the glycerine jelly hardened, and a camera lucida sketch or photograph was made. All of the figures here presented were secured by the latter method. From five to ten preparations of each form were photographed. Blue prints were made from the negatives. The outlines of the tracheæ and veins were then traced directly upon the print. Later the blue color of the paper was bleached out with a saturated solution of potassium oxalate. The ink drawing left upon the white field was then used directly for reproduction.

Historical.

The most important discussions of May-fly wing venation are contained in the following works.

EATON '83 (Revis. Monog. Ephem. '83) divided the veins of the May-fly wing into three groups to which he applied a series of names and numbers as given in the following table. The first group consisted of the longitudinal veins 1 (costa), 2 (subcosta), and 3 (radius), which are all connected by the great cross vein. The second group consisted of veins 4 (sector), 5 (cubitus), 6 (praebrachial) and 7 (pobrachial). The third group consisted of the anal and axillary veins. He called attention to the tendency of the hinder groups to secede from their own set and to annex themselves to the hinder branches of the group next in advance.

REDTENBACHER '86 used Eaton's system but altered it so that it would agree with the theory of convex and concave veins, proposed by Adolph, which Redtenbacher had unfortunately adopted. The May-fly wing was considered to be a very generalized type. Redtenbacher emphasized the relationship between May-flies and dragon-flies, stating that though transitional forms are lacking the wings of the two are so like as to be easily ascribed to a common origin.

COMSTOCK '88 adopted Eaton's system using the same grouping and homologies. He used names instead of numerals in labelling the veins.

COMSTOCK AND KELLOGG '95 built a system upon that of Redtenbacher, but they differed from him in certain particulars as to the homology of some of the veins. These differences are shown in a following table.

KELLOGG '95 reviewed the work of Redtenbacher and Comstock and proposed to further reduce the number of names. The result was a nomenclature which nearly approached that later adopted in the "Wings of Insects." Concerning the remnants of tracheation to be seen in an adult wing of Hexagenia he says: "In a mounted wing of Hexagenia sp. I have plainly observed the branching trachea of the sector arising from the radial trunk at an appreciable distance from the base of the radius." This seems incredible since an examination of many nymphs of this genus have failed to show this.

COMSTOCK AND NEEDHAM '98–'99. In this paper the tracheation of the nymphal wing-pads was discussed for the first time. The wing-veins of the adult were homologized from the tracheæ which preceded them. It was unfortunate that the authors studied only wing-pads in which the bases of the radial and medial tracheæ were approximated, and hence they also fell into the error of considering a part of media to be the radial sector.

For convenience in comparing the various systems of nomenclature I have arranged the following table:

Eaton '83 Rev. Monog. Ephem.	Redtenbacher '86	Comstock '95	Kellogg '95	Comstock-Needham '98	System used in this paper
Costa 1	Costa 1	Costa 1	Costa 1	Costa	Costa
Subcosta 2	Subcosta II	Subcosta II	(Subcosta) II	Subcosta	Subcosta
Radius 3	Radius III_1	Radius III	(Radius) III (R+RS)	Radius	Radius
Radius 4	Radial sector III_2			Radial sector	$Media_1$
	Radial sector III_3			R_3	
	IV	Praemedia IV		Access. radial 1	Rs?
				R_4	Accessory 1
Cubitus 5	Cu VI			R_5	M_2
Praebrachial 6	Praebrachial VII	Media V	V	Media	M_3 and M_4
Postbrachial 7	Postbrachial VIII	Postmedia VI	VII	Cubitus	Cubitus
Anal 8	Anal IX	Cub VII a b		1st Anal	1st Anal
Axil 9_1	Anal X	Anal Furrow VIII	IX	2nd Anal	2nd Anal
Axil 9_2	Axil XI	Anal Vein IX		3rd Anal	3rd Anal

The most generalized tracheation which has been found in May-flies is represented in young stages of the wing-pads of Chirotonetes (Pl. VII, Figs. 33, 34, 35). From these and other generalized wing-pads (especially Pl. V, Figs, 5, 7) the accompanying diagram has been drawn (Fig. 1). The treacheal system of May-flies arises at one point in the longitudinal trachea of the thorax and enters the wing base by a single stem. Near that area which is to be the base of the adult wing the entering stem divides into two trunks. These two trunks remain undivided but a short distance.

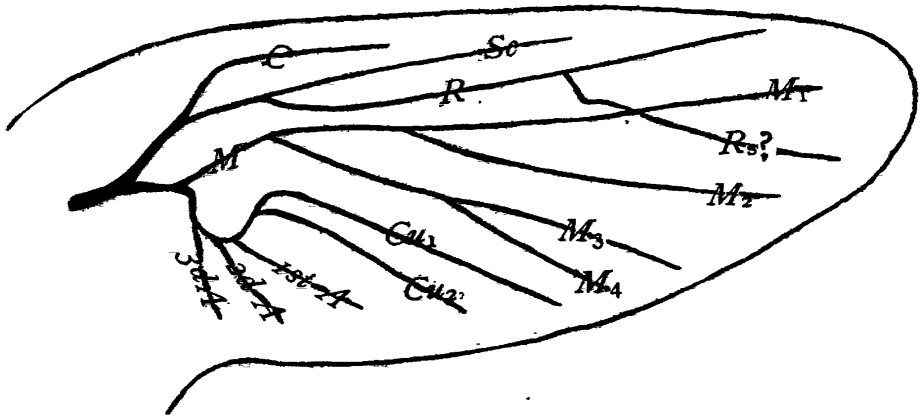

Fig. 1. Tracheation of hypothetical May-fly wing-pad.

The anterior trunk divides into two branches of unequal size. The smaller branch is a delicate trachea which extends forward, and outward parallel with the margin of the wing-pad. This is the costal trachea, (Fig. 1 C). The larger branch divides close to its base into two tracheæ which extend nearly to the margin of the wing-pad. The anterior of these two tracheæ is the sub-costal (Fig. 1, Sc) and the posterior one the radial trachea, (Fig. 1, R).

The foremost branch of the posterior trunk is the medial trachea, (Fig. 1, M). Beyond the point of its separation it divides into four branches. This agrees well with the condition of this vein in insects generally. The posterior branch bends toward the anal margin of the wing-pad. From its basal part three separate branches are given off. These are the 1st, the 2nd and the 3rd anal tracheæ. (Fig. 1, 1st A, 2nd A, 3rd A). A little beyond the 1st anal branch the trachea splits into the two prominent cubital tracheæ. (Fig. 1, Cu_1, and Cu_2).

Peculiarities of May-fly tracheation.

If the tracheation of May-flies (Fig. 1) be compared with the most generalized types of tracheation in other orders several striking peculiarities will be observed.

The radial trachea instead of showing its typical five parts is usually destitute of a sector (cf. Pl. V, Fig. 5 with Figs. 1, 3, 7, etc).

The medial trachea has its characteristic four parts (Pl. V, Fig. 1) but the M_1 trachea bears a branch on the posterior side (labelled R_s ? in the figures) in which it appears to terminate.

If the tracheation in the consecutive figures of the wing-pads in Pls. V, VI, VII, be now examined important differences will be seen. The series shows a continuous reduction of large tracheae and a replacement of them by small tracheal branches. A gradual evolution in the tracheation is thus suggested. An evolution by reduction, which has left some principle tracheæ so reduced as to be hardly recognizable but still holding their proper places.

The Costal and Sub-costal Tracheæ.

The usual course of the costal trachea has been already described. Whenever present in well developed wing-pads it lies without exception in the developing vein which forms the front margin of the wing-pad and which is universally considered to be vein C.

This trachea has been found present as a short, delicate branch in the wing-pads of all but four genera, (Hexagenia, Polymitarcys, Ephemera, Ephemerella, Pl. V, Fig. 13, Pl. VI, Figs. 19, 21, 27). In one, (Ephemerella) this absence may have been due to the rather poor material, but in the others, examinations of many specimens failed to show its presence. The wing-pads of Chirotonetes, Heptagenia, Epeorus, and Iron (Pl. V, Figs. 1, 3, 5, 7, 9,) show a continuous reduction of the costal trachea. In Chirotonetes (Fig. 1) its branches thoroughly aerate the base of the costal region. In the succeeding wing-pads its diminished branching makes the costal trachea less and less important in the aeration of this region. Its work is carried on by branches which spring from the trachea behind it.

The sub-costal trachea is a single usually strong trachea which is parallel to the margin of the wing-pad. It lies in the longitudinal vein posterior to vein C, (Pl. V, Fig. 1). In none

of the wing-pads examined has there been any indication of a splitting of the sub-costal trachea into its two branches Sc_1 and Sc_2.

In the first eleven wing pads in Plates V, VI, (Figs. 1, 3, 5, 7, 9, 11, 13, 15, 17, 19, 21) and in Siphlurus (Pl. VII, Fig. 29) the sub-costal trachea extends to the tips of the wing-pads. It not only aerates its own area, but in some wing-pads it supplies the region before (Pl. VI, Fig. 15), and in others the region before and behind it (Pl. VI, Fig. 17). The sub-costal trachea of Choroterpes, Leptophlebia, and Blasturus (Pl. VI, Figs. 23, 25, 27) has nearly disappeared from its vein and is replaced by branches from the trachea behind it. This condition is similar to that which has already been noted in the costal trachea. It is a further step in the cutting down of main tracheæ.

Radial Trachea.

The remaining branch of the anterior trunk is a simple trachea parallel to the sub-costal trachea. It never deviates from its pathway in the radial vein. This is the radial trachea. It has been found to be unbranched except in one species of Heptagenia (Pl. V, Fig. 5) and in only half of the specimens of this.

In all cases except in Heptagenia (Pl. V, Figs. 3, 5) it is distinct from the medial trachea throughout its course. In Heptagenia both divisions of the main trunk have coalesced at the base so that the radial and medial tracheæ appear to arise from the same stem (Pl. V, Fig. 3, 5).

The development of the radial trachea is variable and its length has important effects upon the aeration of the region behind it. In the more generalized wings (Pl. V, Figs. 1, 3, 5, 7, 9, 11) it extends to the apex of the wing-pad. Ample aeration of the wing-tip is thus provided. In the more specialized wing-pads the radial trachea extends only through the basal third (Pl. V, Fig. 13, Pl. VI, Figs. 15, 17, 19, 21, 27), or has almost disappeared (Pl. VI, Fig. 25).

A progressive development of fine tracheal branches follows the weakening of the radial trachea. When the trachea is reduced its area is aerated by fine branches from the tracheæ before and behind it (Pl. V, Fig. 13, Pl. VI, Figs. 15, 17, 25, 27, Pl. VII, Figs. 29, 31). Thus the place of a main trachea is again taken by secondary branches.

Medial Trachea.

The fullest development of tracheal branches is found in Chirotonetes (Fig. 2). The four typical branches of media are all present and well developed and there is a large accessory trachea attached posteriorly to the M_1 trachea and smaller ones attached posteriorly to M_4. These accessories are usually wanting and need no further consideration. There is however, one peculiarity of the tip of M_1 which is of great importance since it involves the interpretation of the veins in the area between veins M_1 and M_2. Here lies the most difficult problem in the interpretation of May-fly venation.

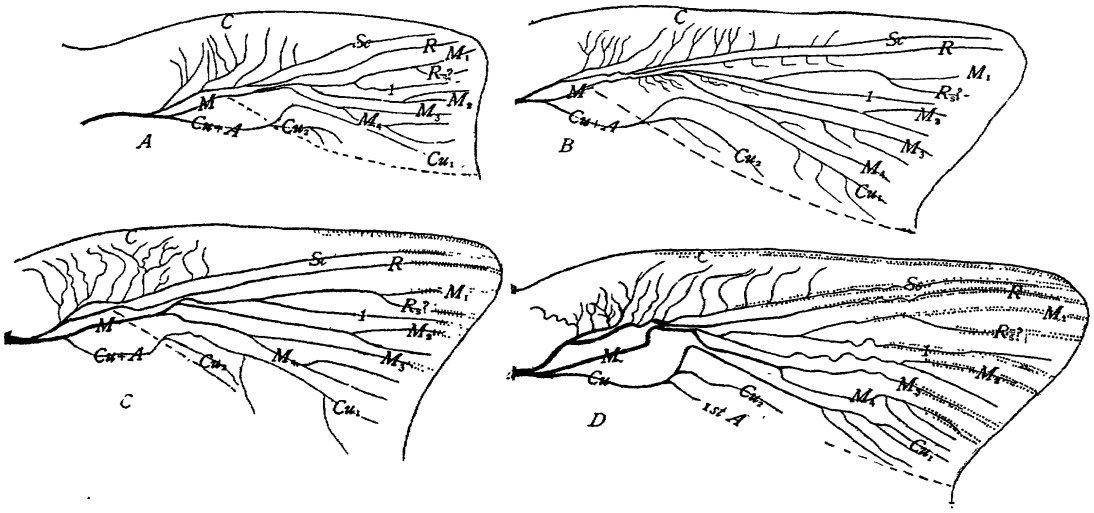

Fig. 2. Tracheation in nymphal wings of Chirotonetes.
A, B, C—Three early stages.
D—Late stage showing venation also.

Trachea M_1 continues through only half its course (Fig. 2, D). An apparent continuation of it turns abruptly rearward and lies in the strong oblique vein Rs?. This condition exists in mature wing-pads of Chirotonetes and in all the most generalized wing-pads, (Pl. V, Figs. 1, 3, 5, 7, 9, 11). In very young wing-pads of Chirotonetes however the M_1 trachea extends through its whole course to the tip of vein M_1, (Fig. 2, A, B, C).

The M_2 trachea lies in the corresponding vein. The M_{3+4} trachea continues for some distance before dividing. It then separates into the two branches M_3 and M_4 which diverge slightly and proceed to the margin in a parallel course.

In Chirotonetes small branches are almost completely absent from the medial tracheæ. In the series of wing-pads

which follow it the progress of the medial trachea from a generalized to a specialized condition is marked by a general development of small tracheoles which aereate this region. This has resulted from the reduction of the main tracheæ. Specialization is also marked by an increasing importance of the forepart of the medial trachea. In this the accessory trachea takes no part, but disappears entirely. The reduction of the tip of the M_1 trachea has taken place because that region is so well aerated by the radial trachea, (Pl. V, Figs. 1, 3, 5, 7, 9, 11). When the radial trachea is greatly reduced (Pl. V, Fig. 13, Pl. VI, Figs. 15, 17, 19, 21, 23, 25, 27) the vein M_1 contains a trachea throughout, although in more generalized forms the terminal portion is wanting, or its area is supplied by tracheoles, (Pl. VII, Figs. 29, 31).

When the costal and sub-costal trachea are also reduced as they are in Choroterpes, Leptophlebia, Blasturus, and Callibætis (Pl. VI, Figs. 23, 25, 27, Pl. VII, Fig. 31) the whole front of the wing is dependent upon branches from the M_1 trachea. With this increase in function the M_1 trachea usually becomes proportionately larger (Pl. VI, Figs. 23, 25, 27) or it gives place to a mesh work of tracheoles (Pl. VII, Fig. 31).

The Accessory_1 (1) disappears early in this series. In Chirotonetes it extends to the margin; in Heptagenia (Pl. V, Fig. 3) it sends a branch over into the tip of vein M_2. In Epeorus (Pl. V, Fig. 7) it has become greatly shortened, and only its stump is left in Iron (Pl. V, Fig. 9). The vein which succeeds it is one of the most prominent accessories in the May-fly wing. In most of the wing-pads this vein is aerated by branches from the tracheæ before and behind it (Pl. V, Fig. 13, Pl. VI, Figs. 15, 17, 23).

The M_2 trachea maintains its full length and gains importance as the tracheæ near it become reduced. In Chirotonetes there is no need for the short posterior branch which it bears, but in Heptagenia (Pl. V, Fig. 5) a branch in approximately the same position aerates vein M_3 and an accessory. This function is similarly performed in Choroterpes and Blasturus, (Pl. VI, Figs. 25, 27) and by means of tracheoles in other wing-pads (Pl. VI, Figs. 15, 17).

If the course of the M_{3+4} trachea be followed through this series it will be seen that there is a continuous reduction of this trachea which ends in its complete obliteration. At first the

M_4 trachea has accessory branches, (Pl. V, Figs. 1, 3). These are lost and the M_3 and M_4 trachea course toward the margin as simple parallel tracheæ (Pl. V, Fig. 7). Later the M_4 trachea becomes reduced (Pl. V, Fig. 9) and ultimately disappears. In Hexagenia (Pl. V, Fig. 13) both the M_3 and M_4 tracheæ have disappeared and a secondary trachea has been developed which lies in the accessory vein between vein M_3 and M_4. A variation of this occurs in Ephemera where the secondary trachea springs from the M_3 trachea (Pl. VI, Fig. 17). In the wing-pads which follow, the M_{3+4} trachea has either nearly disappeared (Leptophlebia and Siphlurus, Pl. VI, Fig. 23, Pl. VII, Fig. 29), or it has become entirely obliterated (Leptophlebia and Callibætis, Figs. 23, 31). In the former cases it is visible in very clear preparations as a small but very distinct trachea lying in the base of vein M_{3+4}. The veins deserted by this trachea are thoroughly aerated by a network of small branches from the tracheæ before and behind. (Pl. VI, Figs. 23, 25; Pl. VII, Figs. 29, 31). Sometimes variable secondary tracheæ from either side (see Blasturus Pl. VI, Fig. 27, and Blasturus Pl. VII, Fig. 40, another specimen) aerate the region between vein M_3 and M_4.

The climax of the changes in the aeration of the medial region is illustrated by the wing-pads of Siphlurus and Callibætis, (Pl. VII, Figs. 29, 31). In the former but two strong tracheæ remain, the M_1 trachea with its apparent continuation and the M_2 trachea. In Callibætis only the M_1 trachea is still strong. All the other tracheæ in the wing-pad are weakened.

The Radial Sector.

In the preceding description no mention of a radial sector has been made, the radial trachea being described as an unbranched trachea and the vein R as an unbranched vein. It is strange that so important an element should be lacking in a wing where the venation is not greatly reduced.

Between M_1 and M_2 there is an undetermined vein which may be an accessory vein or may be the radial sector in an unusual position. This second possibility becomes a very strong probability when we consider what has happened in the Odonata. As has been conclusively shown (Comstock and Needham '98–'99) and (Needham '03) an actual switching of the sector trachea there takes place.

In the dragon-flies (Anisoptera) all stages of this switching are shown. In very young nymphs of dragon-flies the trachea are all separate and in their usual position (Fig. 3A).

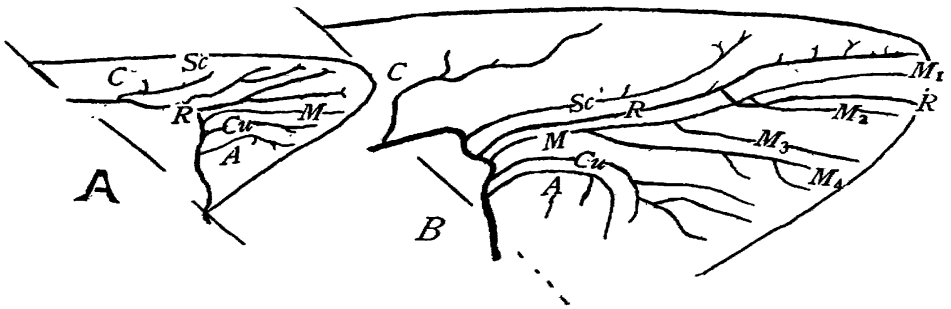

Fig. 3. Two stages of nymphal wings of dragon-fly Gomphus descriptus, after Needham, showing change in position of sector trachea.

In the next stage the radial sector trachea has migrated across the M_1 trachea and reaches the margin between the M_1 and M_2 tracheæ (Fig. 3B). This modification is carried still further in the mature stage where the radial sector is between the M_2 and M_3 trachea. In the adult wing the place where the radial sector crosses over to M_1 is always marked by an oblique cross vein.

In the damsel-flies (Zygoptera) the Rs trachea is always attached to M_1. There is no connection thus far found between the radial trachea and its sector which is completely stranded upon the M_1 tracheae. In the adult wing an oblique cross vein marks the point of crossing over of the sector in only a very few genera.

In May-flies this trachea is one of the most constant features of the tracheation. The vein which follows it is likewise constant in the adult wing. In one species of this series an actual crossing of a strong branch of radius across the M_1 trachea has been found (Fig. V, Pl. 5). A large number of the wing-pads of this species were examined. Half of the wing-pads showed the radial branching just described and half of them gave no sign of it (Pl. VII, Fig. 41). An actual connection between the R and the Rs trachea cannot be shown by constant structures. However, May-flies and dragon-flies are closely allied groups and their general tracheation is similar in many points. Furthermore this condition of the radial sector trachea is exactly the same as that just described in the damsel-flies where there can be no doubt that such a crossing has taken place. It is, therefore,

highly probable that the radial sector is present in May-flies and that both the sector trachea and the vein Rs have been stranded on M_1 and have left no positive trace of their origin.

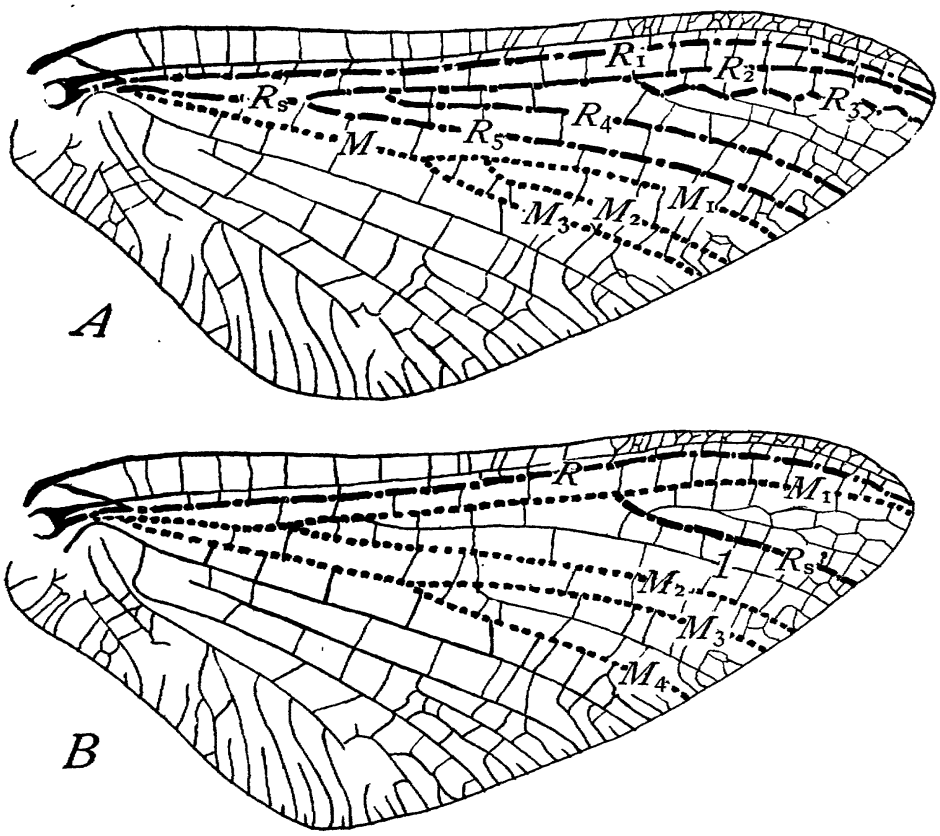

Fig. 4. WINGS OF EPHEMERA.
A. Previous interpretation of radius and media.
B. Present interpretation of radius and media.
Radius and its supposed sector are represented by dots and dashes, media is represented by a series of dots.

Such an interpretation involves important changes in the nomenclature of the veins in the radial and medial regions. These changes may be clearly seen by comparing the wings A and B in the accompanying figure (Fig. 4).

The Cubital Trachea.

In Chirotonetes (Pl. V, Fig. 1) the cubito-anal and medial tracheae diverge and then run nearly parallel for a short distance. In this region the anal tracheae branch off (Pl. V, Fig. 1, 1st A). The cubital trunk then bends forward again toward the medial trachea, making a prominent bend just below the first fork of

media. It soon splits into two branches which extend nearly to the anal margin. These branches are the Cu_1 trachea and the Cu_2 trachea. The Cu_1 trachea lies constantly within the vein directly behind vein M_4 and the Cu_2 trachea within the next primary vein behind Cu_1.

A prominent bend in the cubital trunk is a characteristic feature of May-fly tracheation. Variations of it have been found in all but one (Pl. V, Fig. 5) of the wing-pads examined. (Pl. V, Figs. 7, 9, 11; Pl. VI, Figs. 15, 17; Pl. VII, Fig. 31). In the last case (Callibætis) the cubito-anal stem has joined the general approximation of the tracheal trunks outward and the cubital bend is no longer evident.

The replacement of main tracheæ by small branches is not usual in the cubital region as it is in the radial and medial. It does occur however in Blasturus and Siphlurus (Pl. VI, Fig. 27; Pl. VII, Figs. 29, 40) where small branches of the Cu_1 trachea supply the M_{3+4} vein. With few exceptions (Pl. V, Figs. 1, 3, 7) the cubital trachea are entirely unbranched.

The Anal Tracheæ.

The anal stem is a well defined trachea which splits off from the cubito-anal trunk just before the cubital bend.

In the mature wing-pad of an Ephemera (Pl. VI, Fig. 17) the three anal tracheæ are present. In this wing-pad the 1st A trachea is a strong branch which separates from the distal part of the anal trunk and extends to the margin. It lies in the next primary vein posterior to vein Cu_2. From the posterior side of the 1st A trachea several secondary branches are given off. These are followed by secondary veins. The 2nd A trachea separates from the trunk directly behind the accessory tracheæ. The 3rd anal trachea is a short branch which arises posterior to these accessories. Both the 2nd A and 3rd A tracheæ are followed by primary veins (Pl. VI, Fig. 17). From the evidence presented in the nymphal wing-pads and the wings of the subimago we have considered veins 1st, 2nd, and 3rd A to be typical of May-flies.

In Chirotonetes (Pl. V, Fig. 1) I have been able to demonstrate but one anal trachea. In this and all the other genera examined the anal tracheæ appear much later than those lying farther anterior. This fact accounts for their absence in many of these figures. The first anal trachea has been found in all of

the wing-pads examined and the second in three (Pl. V, Fig. 5; Pl. VI, Fig. 17, Pl. VII, 31). All of the anal tracheæ have been nearly always found in recently emerged sub-imagoes.

Replacement of main tracheæ by small branches does not occur in the anal region. As might be expected, the burden of aeration does not fall here but in the middle region of the wing-pad.

The Tracheal Stem.

As already stated, the single tracheal stem of May-flies is similar to that of no other order, those of other insects as far as known having a dorsal and ventral root (Fig. 5, A. a, b).

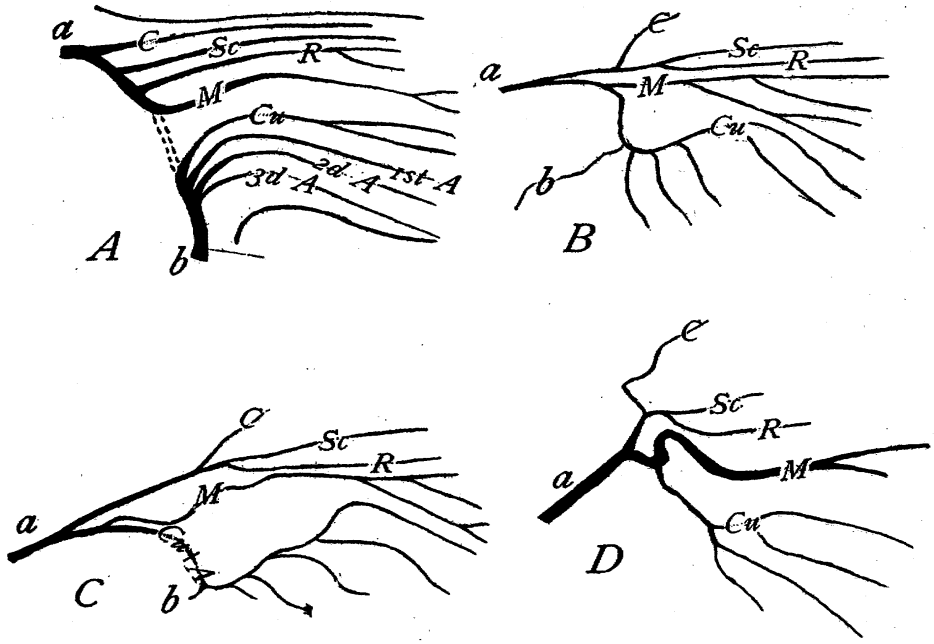

Fig. 5. Diagrams of Tracheal Stems showing shifting of the cubito-anal trachea.
A. Tracheal bases in the hypothetical wing of insects (after Comstock and Needham).
B. In the wing-pad of a hypothetical May-fly.
C. In the generalized wing-pad of Epeorus.
D. In the specialized wing-pad of Callibætis.

In these wing-pads the base of the cubito-anal trachea makes a characteristic prominent downward loop (Fig. 5, B, C). This loop swings the trachea out of the route which it would seem naturally to take. It is more prominent in generalized than in specialized wing-pads (Fig. 5, of C and D).

In some generalized wing-pads a weak branch springs from the cubito-anal loop and extends inward toward the body, nearly parallel with the main stem. (b, in Fig. 5, C). These structures have prompted the suggestion that the weak trachea (b, in Fig. 5, C) may be the remnant of the trachea which connects the trachea of the wing with the ventral body trachea in other orders (b, in Fig. 5, A).

Fossil May-flies.

On account of the difficulty in studying fossil wings only a very brief consideration has been given to them. A few figures of fossil wings believed to be those of May-flies have been copied. (Pl. IX, Figs. 62, 63, 64, 65, 66, 67). The homologies here determined have been applied to these wings. All but the last figure are taken from "Types of Permian Insects" by E. H. Sellards[1]. In these May-flies the fore and hind wings are nearly equal in size, as they are in damsel-flies. The parallel veins of the front part of the wing and the main branches of media are identical with those of modern May-flies. The last figure (Bætis anomala)[2] represents a recent fossil in which the hind wings show the reduction which is the present characteristic of May-flies.

Hind Wings.

The hind-wings of May-flies are greatly reduced in size. In Cænis they are entirely lacking. In consequence of this reduction there are important differences in the front and hind wings. By reason of it also the venation is so reduced as to be of far less value in practical use.

The wing-pads of Chirotonetes show the most generalized tracheation of any which have been studied. In these the bases of the tracheal trunks are similar to those of the front wing (Pl. VIII, Fig. 43). The tracheae however show these differences. The M_1 trachea always extends to the margin of the wing-pad. There is no trace of either the Rs? or the 1st accessory trachea. These veins, however, are present and occupy positions identical with the corresponding veins of the front-wing

[1]E. H. Sellards. Types of Permian Insects. Amer. Jour. of Science, Vol. XXIII, May, 1907. pp. 345–355.

[2]G. C. Berendt. Die im Berstein befindlichen Organischen Rests der Vorwelt. 1856. Zweiter Band. Abt. II. Neuropteren (Pictet Baraban & Hagen). Tab. VI, Fig. 1.

In the wing-pads figured in Pl. VIII, there is a gradual reduction of the main trachea in the front of the wing. This is shown first in Heptagenia (Pl. VIII, Fig. 45) where the base of the subcostal trachea has apparently fused with the radial trachea, later by its total obliteration, (Pl. VIII, Fig. 51). In all of these except Callibætis the Sc has been the only vein to disappear (Pl. VIII, Figs. 46, 48, 50, 54). Between M_1 and M_2 there are several accessory veins which are generally bent backward and attached to the vein next posterior. The direction of their bending is just the opposite of these same accessories in the fore-wing.

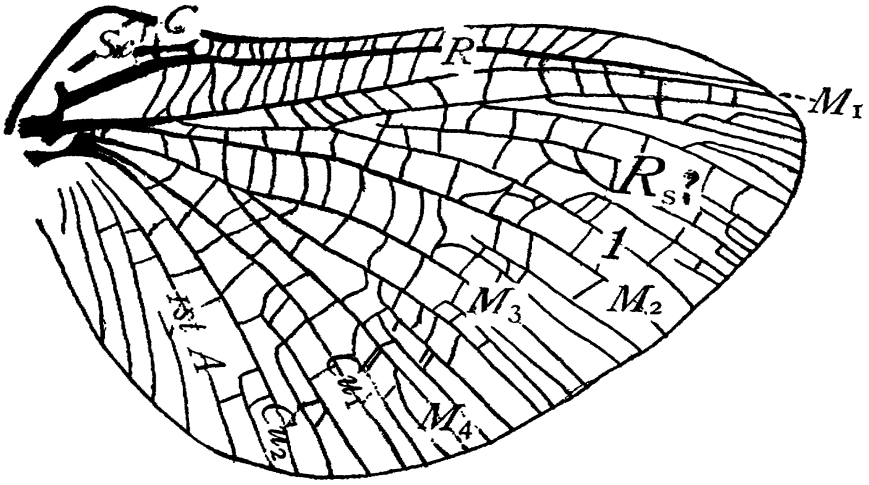

Fig. 6. Hind wing of Palingenia longicauda Oliv. (After Eaton.)

The direction and the attachment of these accessories was traced through a series of hind-wings. In a few of the generalized wings they were bent forward and attached to vein M_1 (Palingenia, Fig. 6) like the similar accessories of the fore-wing. Between this anterior attachment to M_1 and the posterior joining to M_2 figured in Heptagenia (Pl. VIII, Fig. 46) there were many intermediate positions. One of these is represented by Chirotonetes (Pl. VIII, Fig. 44). We may conclude then that the wing of Palingenia represents a generalized type of the hind wing in which a number of accessory veins are joined to M_1 and M_2 is a simple vein. This condition is very near to that in the fore-wing. By a general shifting backward the accessory veins have been thrown upon vein M_2 and have thus made it secondarily a branched vein. There are 3 sizes of

intercalaries as in front wing. The hindmost is longest as in front-wing, two others are of intermediate length. The Acc_1, and Rs? are in positions identical with the corresponding veins of the front wing. Sub-costa is much reduced; in most cases entirely wanting. In Palingenia (Fig. 6, Sc) it is a strong but very short vein.

Summary.

This is a study of the ontogeny of wings representing fifteen genera of May-flies in which the following facts are shown:

1. The main veins of May-flies may be homologized with the veins of insects of other orders.

2. The main tracheæ precede and constantly mark the course of the main veins.

3. The costal and subcostal tracheæ are simple and parallel as are the veins which follow them.

4. The radial trachea (except in one form studied) and the vein which follows it are unbranched.

5. The radial sector is very probably present in May-flies but in an unusual position between the veins M_1 and M_2. It is detached from radius, as in the dragon-flies, and stranded upon vein M_1.

6. The medial trachea and the vein M show four branches which are characteristic of media in its primitive condition. It is similar to the media in the closely allied dragon-flies.

7. The tracheal system enters the wing by a single stem. The course of the cubito-anal trunk shows a possible trace of the double stem of the tracheal system of other orders.

8. In the series of wing-pads studied a remarkable evolution of tracheation is shown. This evolution consists of a gradual reduction of main tracheæ and replacement by small branches.

9. This interpretation of the venation involves the important changes of nomenclature shown in Fig. 4.

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EXPLANATION OF PLATES.

Plate V.

(In the wing-pads continuous lines represent tracheae and tracheoles; dotted lines represent developing veins.)

Fig. 1. Wing-pad of Chirotonetes albomanicatus. Needham.
" 2. Wing of " "
" 3. Wing-pad of Heptagenia sp.?
" 4. Wing of "
" 5. Wing-pad of Heptagenia sp. (nymph No. 3 Needham).
" 6. Wing of "
" 7. Wing-pad of Epeorus humeralis Morgan.
" 8. Wing of " "
" 9. Wing-pad of Iron fragilis Morgan.
" 10. Wing of " "
" 11. Wing-pad of Ameletus ludens Needham.
" 12. Wing of " "
" 13. Wing-pad of Hexagenia sp.?
" 14. Wing of " "

Plate VI.

Fig. 15. Wing-pad of Polymitarcys albus Say.
" 16. Wing of "
" 17. Wing-pad of Ephemera sp.
" 18. Wing of "
" 19. Wing-pad of Caenis diminuta Walker.
" 20. Wing of " "
" 21. Wing-pad of Ephemerella rotunda Morgan.
" 22. Wing of " "
" 23. Wing-pad of Leptophlebia sp?
" 24. Wing of "
" 25. Wing-pad of Choroterpes sp?
" 26. Wing of "
" 27. Wing-pad of Blasturus cupidus Say.
" 28. Wing of " "

PLATE VII.

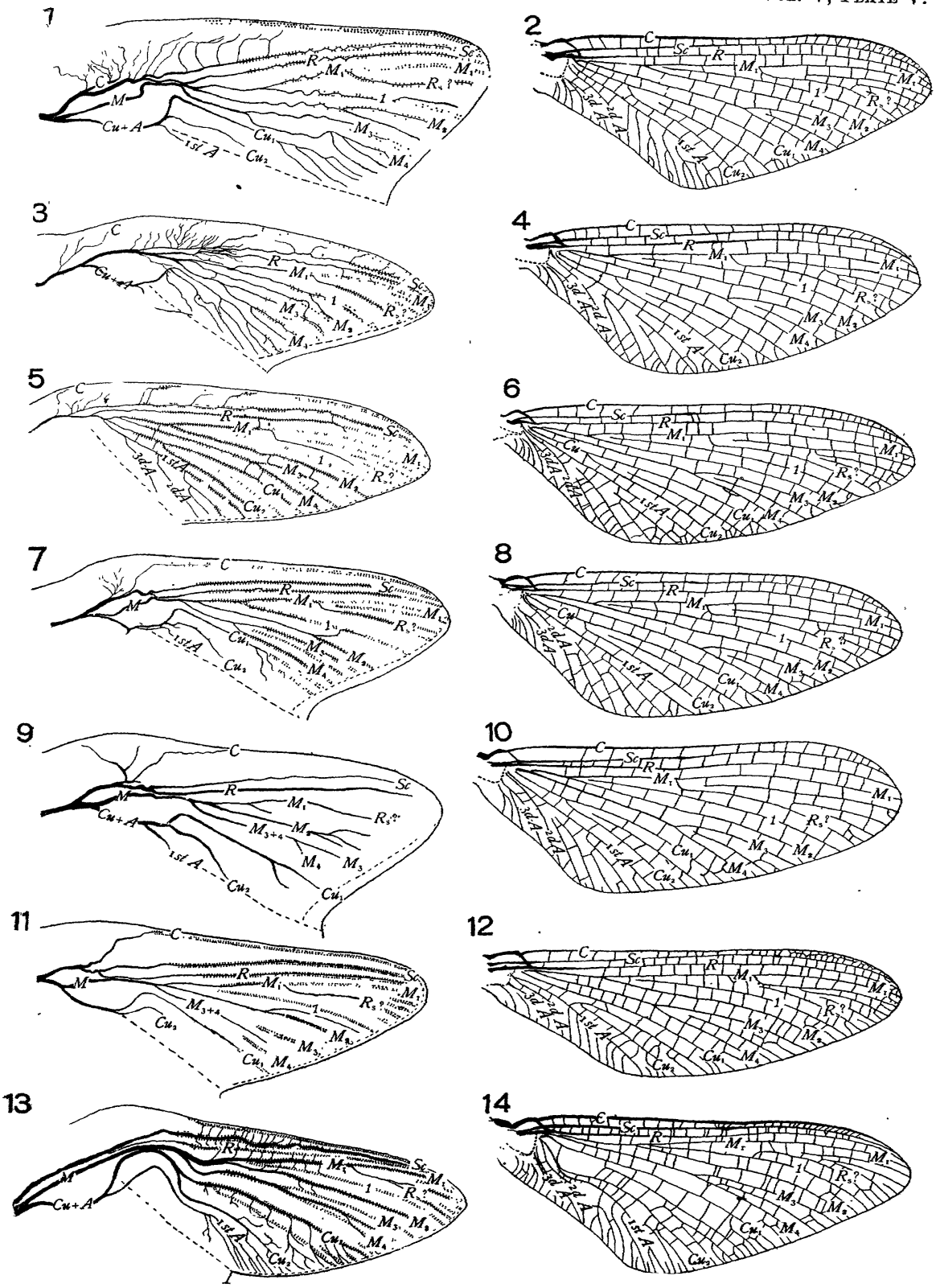
Fig. 29. Wing-pad of Siphlurus sp?
" 30. Wing of "
" 31. Wing-pad of Callibaetis sp?
" 32. Wing of "
" 33.
" 34. } Successive stages of wing-pads of Chirotonetes albomanicatus Needham.
" 35.
" 36.
" 37. } Successive stages of wing-pads of Blasturus cupidus Say.
" 38.
" 39. Base of wing-pad of Hexagenia sp?
" 40. Wing-pad of Blasturus cupidus showing variation in aeration.
" 41. Wing-pad of Heptagenia sp? (No. 3 Needham). showing variation in Rs?
" 42. Wing-pad of Ephemera showing slight variation in tracheation.

PLATE VIII.

Fig. 43. Hind wing-pad of Chirotontes albomanicatus Needham.
" 44. " wing of " "
" 45. " wing-pad of Heptagenia sp?
" 46. " wing "
" 47. " wing-pad of " sp? (Nymph No. 3, Needham).
" 48. " wing of "
" 49. " wing-pad of Epeorus humeralis Morgan.
" 50. " wing of " "
" 51. " wing-pad of Callibaetis sp?
" 52. " wing of "
" 53. " wing-pad of Leptophlebia sp?
" 54. " wing of "

PLATE IX.

Fig. 55. Wing of Potamanthus luteus (after Eaton).
" 56. " Calliarcys humilis "
" 57. " Tricorythus (Malay sp.) "
" 58. " Spanophlebia Trailiæ. "
" 59. " Lachlania abnormis "
" 60. " Oligoneuria rhenana "
" 61. " Elassoneuria Trimeniana "
" 62. Fossil May-fly. Type of genus Protereisma (after Sellards).
" 63. " " Wing of Prodromus rectus "
" 64. " " Wing of Protereisma minus "
" 65. " " Wing of Protechma accuminatum "
" 66. " " Wing of Rekter arcuatus "
" 67. " " Baetis anomala (after Pictet-Baraban and Hagen).



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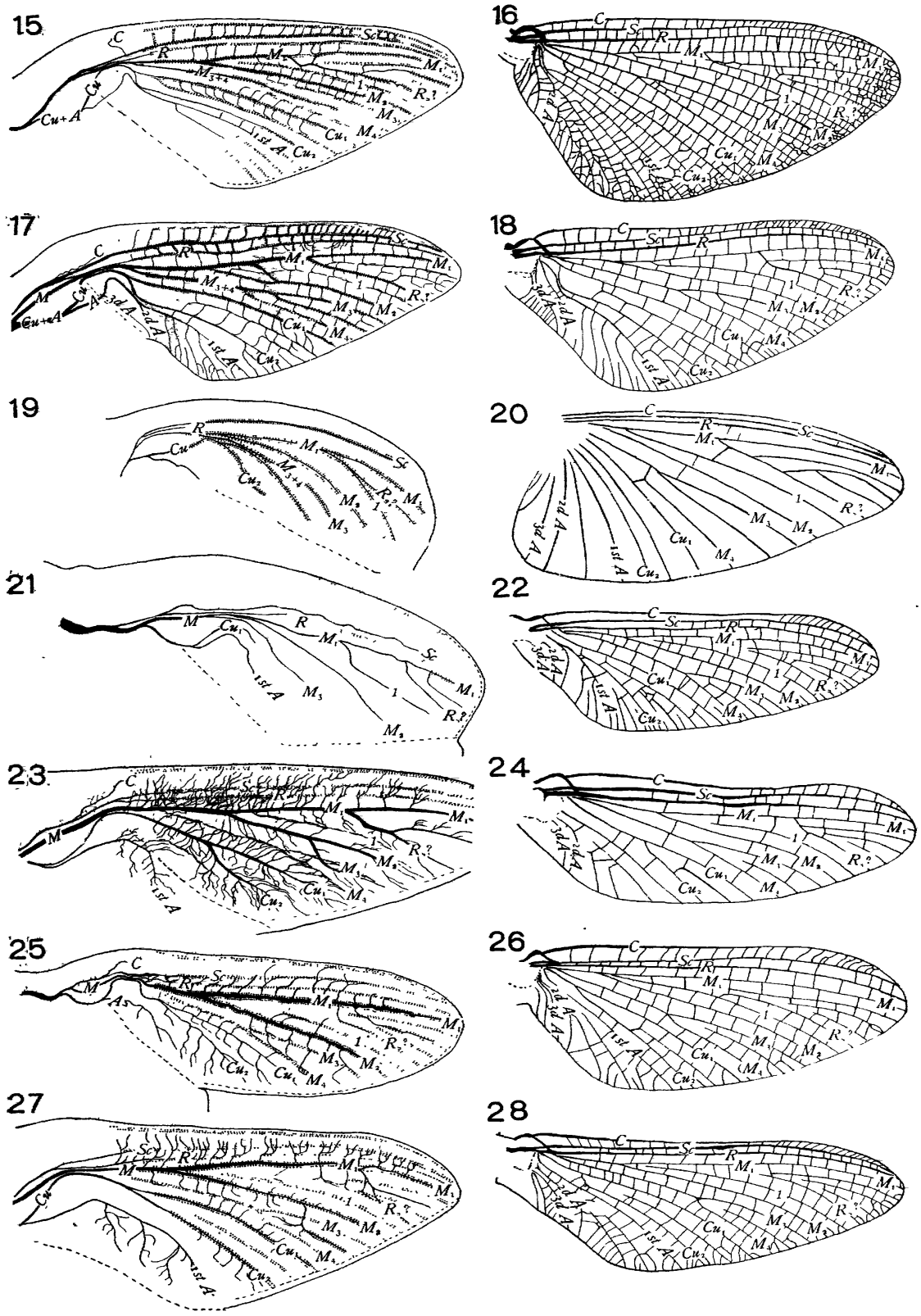

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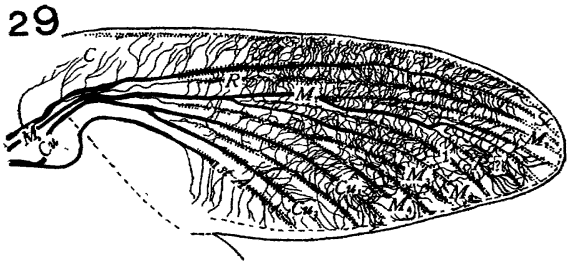

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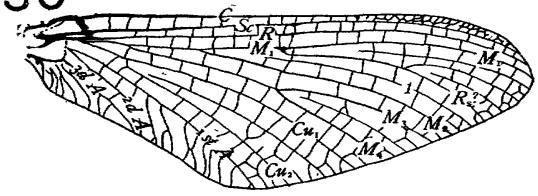

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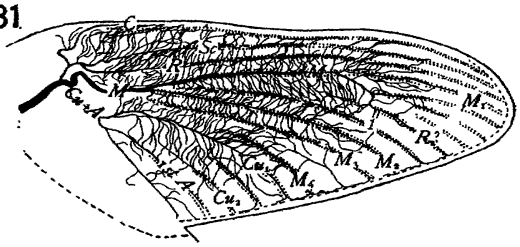

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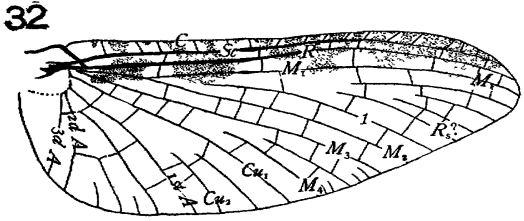

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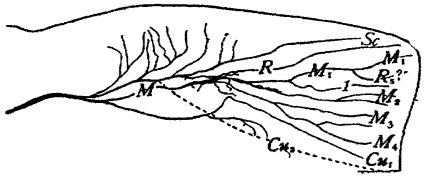

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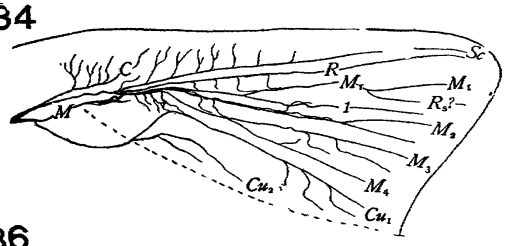

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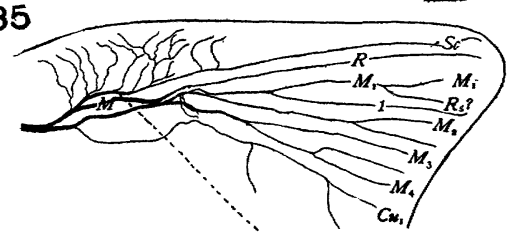

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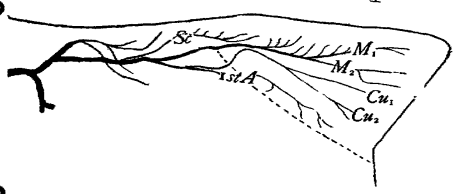

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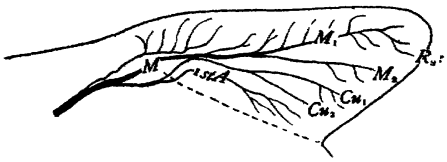

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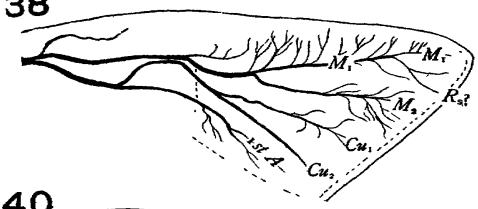

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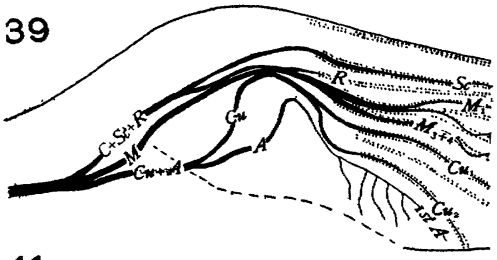

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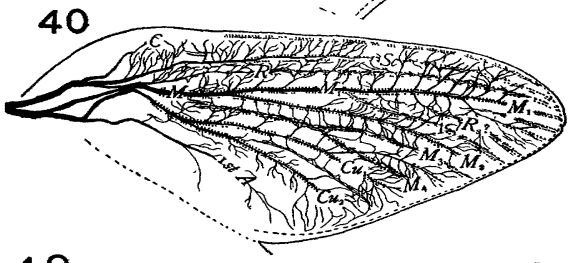

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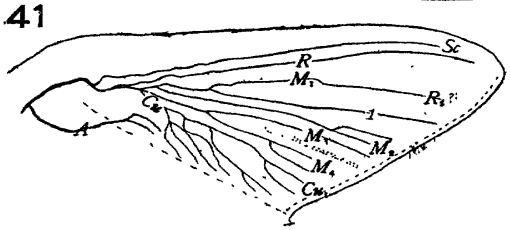

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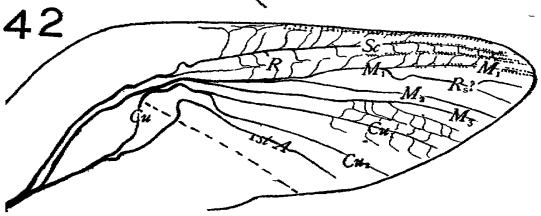

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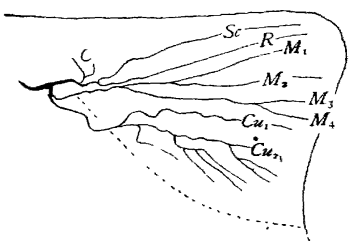

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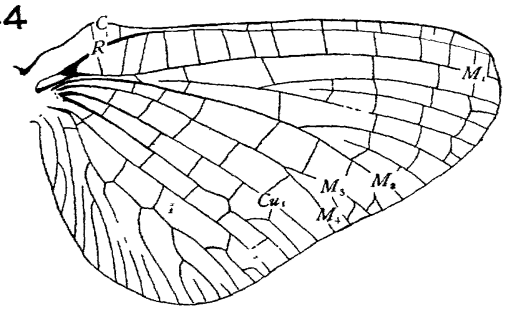

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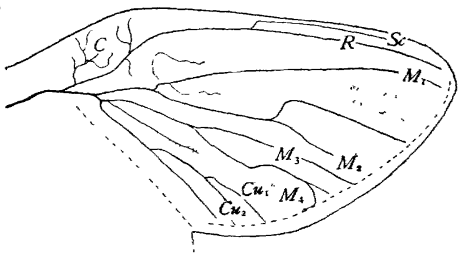

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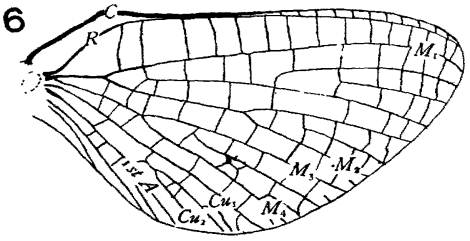

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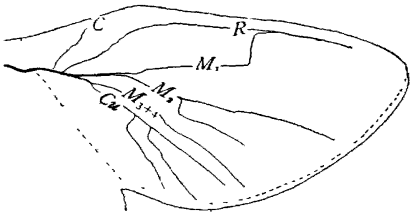

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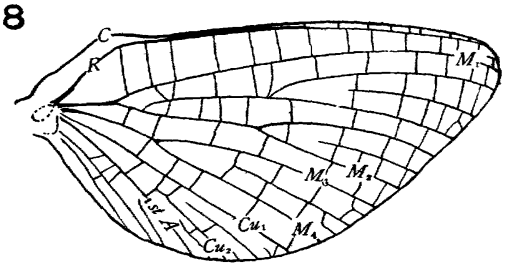

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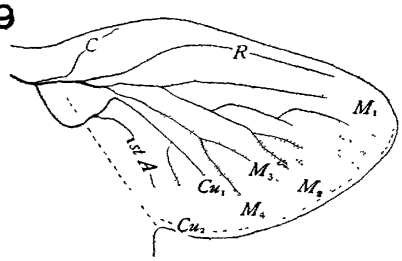

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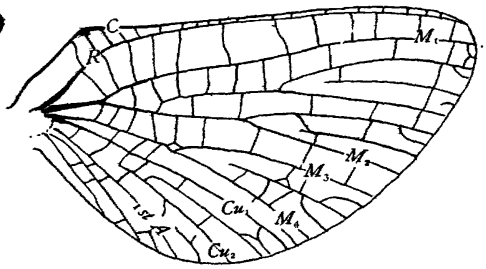

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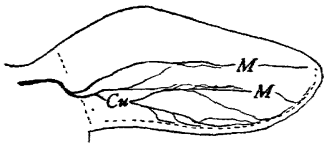

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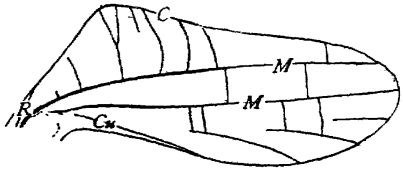

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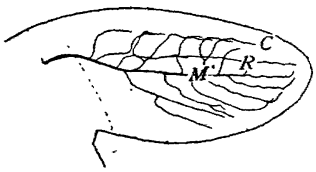

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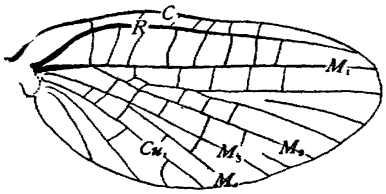

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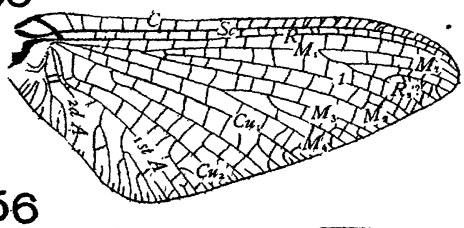

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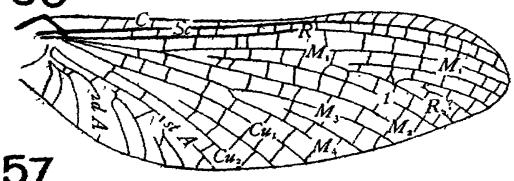

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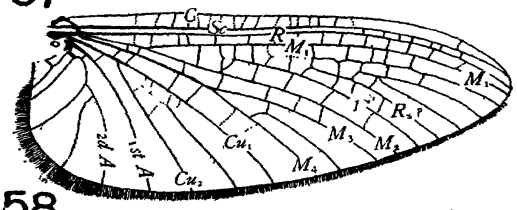

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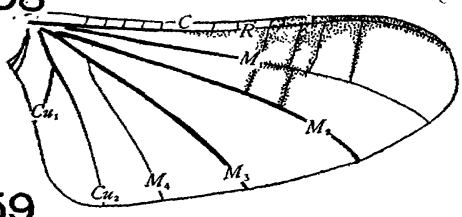

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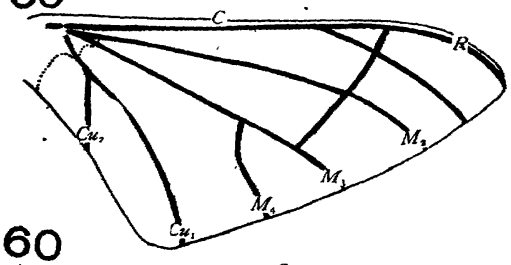

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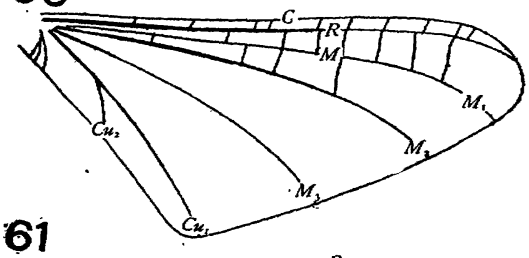

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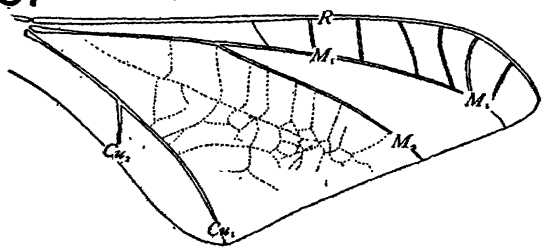

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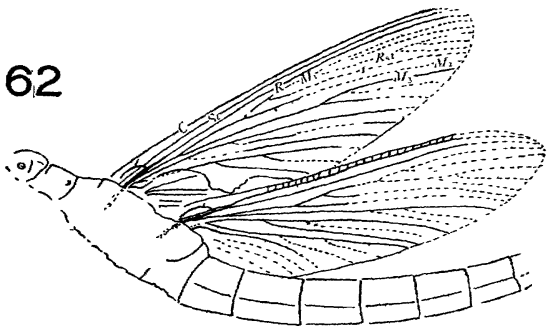

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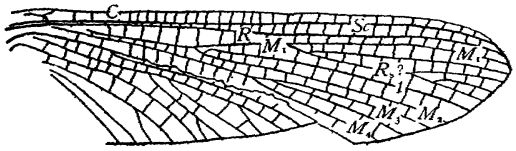

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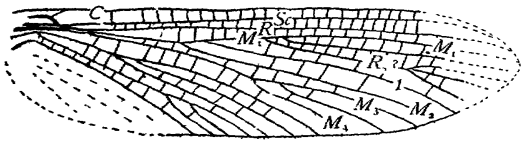

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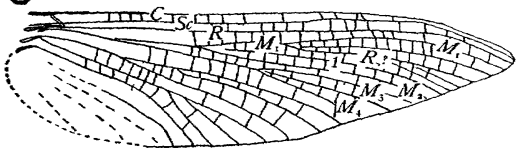

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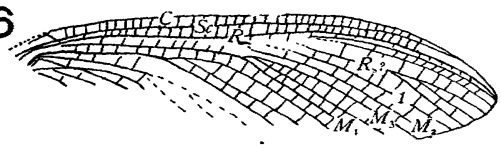

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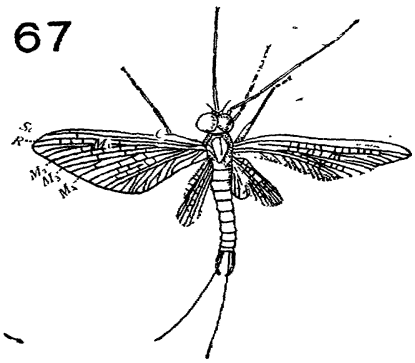

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