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The Wing-Venation of the Order Plectoptera or Mayflies. By R. J. TILLYARD, M.A., Sc.D.(Cantab.), D.Sc.(Sydney), F.L.S., C.M.Z.S., F.E.S., Entomologist and Chief of the Biological Department, Cawthron Institute, Nelson, N.Z.

(With 10 Text-figures.)

[Read 30th November, 1922.]

THE present paper is intended to be read in conjunction with the series of papers being prepared by me on the Wing-Venation of the Order Odonata or Dragonflies, the first of which has already been published (Tillyard, 1922), the remainder having been kept back to allow of the present results being considered first.

At the present time, considerable doubt appears to exist as to the true interpretation of the homologies of the wing-veins in Mayflies. This is not to be wondered at when we consider that Comstock and Needham originally offered one interpretation (1899), which became widely accepted, but that, following on Needham's discovery (1903) of the crossing-over of the supposed Rs in Anisopterous Dragonflies, Miss Anna Morgan (1912), working clearly under the influence of this discovery, offered a new interpretation bringing the venation of the Mayflies into line with that of the Dragonflies in this very important respect, although the evidence brought forward in her paper to support this view is admittedly of the slenderest kind. Space will not allow us to give here a full critical discussion of Miss Morgan's paper. It will only be necessary to make a single quotation from it, as follows (*l. c. p. 98*) :—

“An actual connection between R and Rs trachea (in Mayflies) cannot be shown by constant structures. Moreover, Mayflies and Dragonflies 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 Mayflies, 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.”

On these very slender and debatable grounds, Miss Morgan proceeded to alter the homologies of the wing-veins in the Order. While recognising and admiring the painstaking work shown in her study of the tracheation and venation of so many little-known types, we have to confess that, like Prof. MacGillivray, under whom the work was done (*l. c. p. 89*), we “disagree with some of the interpretations . . . presented.”

Now that I have shown the strong improbability that the supposed Rs of Needham in the Anisoptera is really not that vein (Tillyard, 1922), and definite proof is forthcoming that, in the Zygoptera, the supposed Rs never

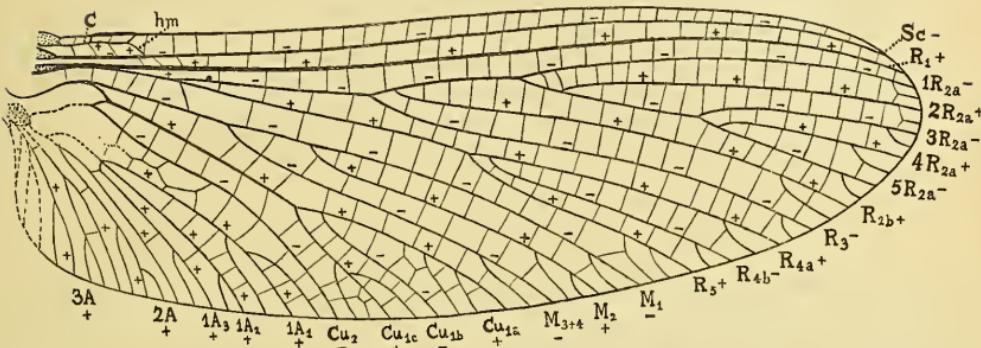
had any connection with R at all, and is most certainly not that vein, any system of homologies based on these results of Needham in the Odonata becomes so highly speculative in character as to cease to attract even those who may have originally accepted it. It is, therefore, necessary to enquire anew into the whole question of the homologies of the wing-veins of the Order. This I have attempted to do during the last three years. The results obtained appear to me to show, not only that the system proposed by Miss Morgan was incorrect, but that the original system proposed by Comstock and Needham (1899) was also wrong, and that the true interpretation of the homologies is one hitherto unsuspected in any quarter. These results, again, also support some startling new results obtained for the Odonata ; and it is for that reason that the publication of the present paper is interpolated between the first and second papers of the series on that Order.

For the purpose of obtaining a really trustworthy result in an admittedly difficult problem, I have attempted to combine three methods of study, viz. : (1) the study of the Palaeozoic Mayflies ; (2) the study of the nymphal tracheation in archaic existing types ; and (3) the application of the principles of convex and concave veins, both to fossil and recent forms. Good fortune favoured this plan. In the first place, when visiting New Zealand in 1919-20, Prof. C. Chilton, of Canterbury College, Christchurch, very kindly accompanied me on a visit to the Cass Biological Station, which is under his charge. Here we found abundant material of the larvæ of the archaic types of Siphluridæ for which New Zealand is famous. As all the necessary apparatus for dissections and microscopic study were at hand in the Station, I was able to make a thorough study of these larvæ on the spot. This produced a surprise, in that the tracheation was found to be almost complete in the various instars, and fairly easy of interpretation ; whereas, in the Mayflies studied by Miss Morgan, the tracheation was both incomplete and irregular. Following on this discovery, during my visit to America in 1920, through the kindness of Prof. C. Schuchert, I studied the Lower Permian fossils left behind by Dr. Sellards in Yale University, and was surprised to find among them a very fine specimen of *Prottereisma*, so beautifully preserved that it at once gave me the key to the whole venation of the Order, and, incidentally, supported the evidence given by the study of the larval tracheation. It then became clear to me that, if the significance of the alternation of convex and concave veins had been fully understood, and applied to the solution of this problem, the homologies would at once have become perfectly clear. In his paper on the Lower Permian Mayflies, Sellards (1907) entirely ignored this important point. Consequently, no help was to be obtained from his work by Miss Morgan, and she merely contents herself with copying his figures (1912, pl. 9. figs. 62-66), and attaching thereto the results obtained by her own researches.

Text-fig. 1a shows the hind-wing of a species of *Prottereisma* with the homologies of the veins obtained by this new method of study. For

purposes of comparison the fore-wing of *Ameletus ornatus* is placed on p. 146 (text-fig. 1b). The corresponding notations of Comstock-Needham and Morgan are given in the accompanying table. In the second column the alternate convexity and concavity of these veins is indicated by the signs + and -.

TEXT-FIG. 1 a.



Hind-wing of *Protereisma* sp., Lower Permian of Kansas; the fore-wing is closely similar, but a little narrower at base, as shown in text-fig. 3.

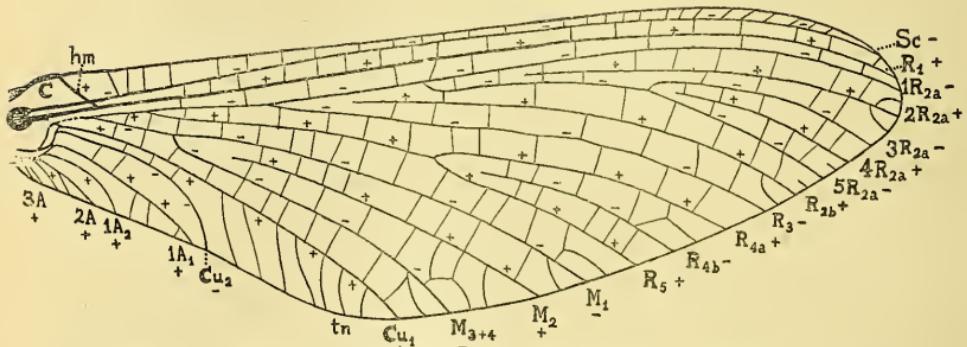
TABLE OF WING-VENATION OF MAYFLIES.

New Notation.	Sign.	Comstock-Needham Notation.	Morgan's Notation.
C	+	C	C
Sc	-	Sc	Sc
R <sub>1</sub>	+	R <sub>1</sub>	R <sub>1</sub>
1R <sub>2a</sub>	-	R <sub>2</sub>	M <sub>1</sub>
2R <sub>2a</sub>	+	(omitted)	(omitted)
3R <sub>2a</sub>	-	(omitted)	(omitted)
4R <sub>2a</sub>	+	(omitted)	(omitted)
5R <sub>2a</sub>	-	R <sub>3</sub>	R <sub>s</sub>
R <sub>2b</sub>	+	R <sub>4</sub>	Interpolated vein 1.
R <sub>3</sub>	-	R <sub>5</sub>	M <sub>2</sub>
R <sub>4a</sub>	+	M <sub>1</sub>	M <sub>3</sub>
R <sub>4b</sub>	-	M <sub>2</sub>	(omitted)
R <sub>5</sub>	+	M <sub>3</sub>	M <sub>4</sub>
M <sub>1</sub>	-	Cn <sub>1</sub>	Cu <sub>1</sub>
M <sub>2</sub>	+	Interpolated vein.	Interpolated vein.
M <sub>3+4</sub>	-	Cu <sub>2</sub>	Cu <sub>2</sub>
Cu <sub>1</sub>	+	1A	1A
Cu <sub>2</sub>	-	2A	2A
1A	+	3A	3A
2A	+	3A	3A
3A	+	3A	3A

It will be noticed that no less than five branches of  $R_{2a}$  are indicated in the new notation. An explanation of this will be found in the argument on page 148 concerning the nature of triads.

The results obtained by the three methods of study, already mentioned, support one another, except that in the case of the study of the larval tracheation a certain amount of variation is normally present. I have therefore presented the argument based on the Convexity and Concavity of the veins first, followed by that deduced from the study of these conditions as noted in the fossil *Prottereisma*, and have kept for the last place the results obtained from the larval trachea. In dealing with these last, the alternative interpretations given in the table on p. 145 will be considered, and reasons given for rejecting them.

TEXT-FIG. 1b.



Fore-wing of *Ameletus ornatus* (Eaton), Recent, for comparison with text-fig. 1a.  $tn$ , tornus.  
Lettering as on p. 162.

#### CONVEX AND CONCAVE WINGS.

In all generalised insects, we are able to distinguish the presence of two kinds of veins on the wings, viz. those which occupy the summits of ridges, commonly called *convex veins* (indicated by a *plus sign*), and those which lie in the bottoms of grooves or hollows, commonly called *concave veins* (indicated by a *minus sign*). In the ideal archetypic wing, convex and concave veins follow one another alternately across the main portion of the wing, Sc being  $-$ ,  $R_1$  and its sector  $+$ ,  $M$   $-$ , the vein commonly called  $Cu_1$   $+$ , and  $Cu_2$   $-$ . This last is always to be distinguished by lying either in or very closely anterior to the deep *anal furrow*, which separates off the *clavus* or *anal area* from the rest of the wing. The clavus itself is a *wholly convex* area, and carries only convex veins, viz. the three anal veins  $1A$ ,  $2A$ , and  $3A$ . In an ideal forked vein, both branches of the fork keep the same condition of convexity or concavity as the main stem; but the alternation of ridge and

hollow is preserved, in the case of areas broad enough, by the development of intermediate branches which take the opposite condition to the two branches which they separate. These have been considered as *interpolated veins* in the Mayflies; *i.e.*, they have been supposed to develop from the margin of the wings inwards, and not to be true branches of the main veins at all. A study of the fossil Mayflies shows, however, that originally there were no interpolated veins in this Order at all, and that the discontinuity of these veins has been brought about actually by absorption of the basal connections with the veins of which they are true branches.

The primitive system of branching which is shown almost to perfection in the Permian Mayflies is the type which we may conveniently term the *triad*. This can be understood from text-fig. 2. V is a convex vein which divides

TEXT-FIG. 2.

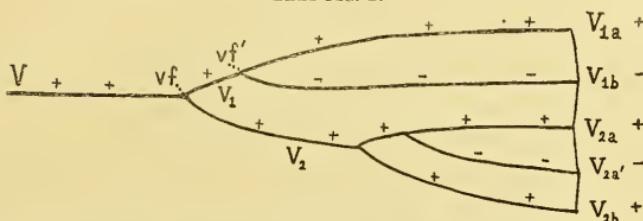


Diagram of the triadic system of branching of main veins. For explanation, see text.

at its primary fork  $vf'$  into two equally convex branches  $V_1$  and  $V_2$ . In the diverging angle between these two, a concave vein arises from either  $V_1$  or  $V_2$ , its point of origin being not far distad from  $vf'$ ; this secondary fork is termed  $vf''$ . In the illustration before us, the concave vein is made to arise from  $V_1$ , so that the two branches of this vein become  $V_{1a}$  (+),  $V_{1b}$  (-), and  $V_2$  (+). If, instead of being a convex vein,  $V$  were a concave vein, then the two branches  $V_1$  and  $V_2$  would be concave, and the intermediate vein  $V_{1b}$  would be convex. The two cases can be distinguished by calling the triad developed from an originally convex vein a *positive triad*, that from an originally concave vein a *negative triad*.

Further branching may take place from any one of the three veins of a triad, and usually consists of the development of further triads. In text-fig. 2, a further triad is seen developed from  $V_2$ , viz. the positive triad  $V_{2a}$  (+),  $V_{2a'}$  (-), and  $V_{2b}$  (+). If a triad had been developed from  $V_{1b}$ , it would have been a negative triad, and the notation used would have been  $1V_{1b}$  (-),  $2V_{1b}$  (+), and  $3V_{1b}$  (-); this notation was chosen to avoid duplication of suffixes.

We can now see what has happened to the radius in *Protereisma*. This vein is convex, and divides first of all into a positive triad,  $R_1$  (+),  $R_{2+3}$  (-), and  $R_{4+5}$  (+). The negative member of this group,  $R_{2+3}$ , next develops a

negative triad, viz.  $R_{2a}(-)$ ,  $R_{2b}(+)$ , and  $R_3(-)$ . The second and third members of this triad remain unbranched to the margin; but the first,  $R_{2a}$ , develops another negative triad, from the third branch of which a further negative triad is also developed. To save complications in the notation, I have named the five veins developed on the wing-margin by these two latter triads  $1R_{2a}$ ,  $2R_{2a}$ ,  $3R_{2a}$ ,  $4R_{2a}$  and  $5R_{2a}$ ; it will be noticed that they are alternately concave and convex.

The triad system, as will be clearly seen, always results in the formation of alternately convex and concave veins along the wing-margin. There is a large body of evidence to show that, apart from the Mayflies, this system was the original system of branching of the veins in the insect wing. Consideration of this evidence is beyond the scope of this paper, but attention is drawn to it in the hope that students of other Orders will attempt to recognise the remains of triads in the wings before them. As examples of archaic triads, we may take the universally recognised primitive set of three branches of  $R$ , viz.,  $R_1$ ,  $R_{2+3}$ ,  $R_{4+5}$ , which is formed from an original positive triad with the intermediate vein developed from the lower branch  $Rs$ . A similar archaic triad appears also to have developed from  $M$ , viz.  $M_1(-)$ ,  $M_2(+)$ , and  $M_{3+4}(-)$ , as shown in *Prottereisma*, though this triad often appears in other insects as  $M_{1+2}(-)$ ,  $M_3(+)$ , and  $M_4(-)$ , owing to a difference in the position of the origin of the intermediate vein. It will readily be seen how easily a pectinate series can be developed from the triadic system; an example of this can be seen in the vein  $Cu_1$  in *Prottereisma*. Simple dichotomies, on the other hand, may be explained by either the non-development or suppression of the middle member of a triad, as in the case of the secondary branches of  $Rs$  in most insects.

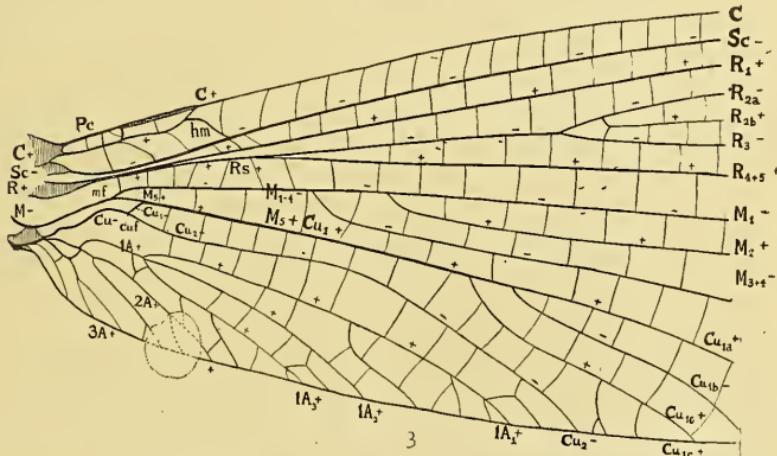
We now pass from the consideration of the triad to the application of the rule of alternate convexity and concavity of veins as it affects the problem of the elucidation of the homologies of the wing-veins in an archaic Mayfly such as *Prottereisma* (text-figs. 1, 3). The general rules applicable to all except very highly-specialised wing-types may be stated as follows:—

- (1) Two strongly convex veins can always be recognised lying between the costal margin and the anal furrow, viz.,  $R_1$  and  $Cu_1$ .
- (2) The concave vein lying between  $R_1$  and the costal margin is  $Sc$ .
- (3)  $M$  is a weakly concave vein lying between two ridges of  $R_1$  and  $Cu_1$ . In many archaic types it gives off a posterior branch close to the base, which joins with  $Cu_1$ , thus forming the *cubito-median Y-vein*, the main stem of which is properly denoted by  $M_5+Cu_1$ , though usually called simply  $Cu_1$ . If this Y-vein can be recognised, any doubts as to the limits of  $M$  and  $Rs$  should be finally removed.
- (4) The vein lying either in or slightly anterior to the *anal furrow* is the *vena dividens*,  $Cu_2$ .

(5) The clavus or anal area is a wholly convex area, and may carry from one to three convex anal veins, any of which may be branched or simple.

Applying these rules to a well-preserved specimen of *Prottereisma*, such as the one figured in text-fig. 3, which Prof. Schuchert kindly allowed me to keep for study during the last two years, the archaic condition of the wing-venation is clearly shown in that the application of all five of the above rules can be made without any doubt or hesitation. The high ridge of  $R_1$  can be found at once with the concave vein  $Sc$  lying anterior to it. At the base of the wing there is developed a short convex vein between  $Sc$  and the costal border. This must be considered as a true primitive costal vein,  $C$ , not a basal branch of  $Sc$ , since it is convex and not concave. Sellards (1907) has already shown how it forms a brace for the costal border, and has its homologue in existing Mayflies.

TEXT-FIG. 3.



Basal portion of fore-wing of *Prottereisma* sp., Lower Permian of Kansas, considerably enlarged to show details of venation. Note the cubito-median Y-vein having  $M_1$  as upper arm,  $Cu_1$  as lower arm, and  $M_5+Cu_1$  as main stem. For lettering, see p. 162.

We should next set about determining  $Cu_1$ , the anal furrow and the clavus, keeping the consideration of  $M$  and  $Rs$  until the last, as it is the limits of these veins which have been the chief trouble in the past. Again returning to our specimen of *Prottereisma*, we find that the only vein which satisfies the conditions for  $Cu_1$  is that which has previously been called  $1A$ , and that its concave branch  $Cu_2$  can be clearly seen running in the anal furrow with a characteristic curve basally, and separating off from the rest of the wing a small, but quite distinct, convex clavus on which only convex veins are

present. In order to test this conclusion, we next look for the cubito-median Y-vein, and find that it is present quite close to the base of the wing in the very characteristic form shown in text-fig. 3. This definitely determines the correct homology of the vein  $M_5 + Cu_1$ , and enables us to pick up at once the true median above it, viz. the concave vein which had previously been called  $Cu_1$ , in spite of the fact that it is not convex. We thus find that  $M$  is a three-branched vein, excluding  $M_5$ , of triadic type, just as it is in so many of the Palaeodictyoptera themselves.

We now have only the limits of  $Rs$  to consider. The whole of the many-branched vein which had previously been considered to be formed of  $Rs$  and  $M$ , combined by basal fusion, is now seen to belong to  $Rs$  alone. It arises from  $R_1$  near the base, and its short basal piece is convex. It then branches into a concave upper branch ( $R_{2+3}$ ) and a convex lower one ( $R_{4+5}$ ); and thus, as already indicated above, it makes with  $R_1$  a true positive triad. The numerous branchings of  $Rs$  shown in *Prottereisma* need not be a cause of wonder, since they are paralleled in quite a number of Palaeodictyopterous types.

In text-figs. 1 and 3, it should be noted that, excluding the clavus, on which all the veins are convex, the whole of the veins reaching the wing-margin are placed alternately convex and concave. The complete notation for the wing of *Prottereisma* has been already given in the table on p. 145.

#### COMPARISON OF THE VENATIONS OF FOSSIL AND RECENT MAYFLIES.

The next step is to make a careful comparison between the venation of fossil Mayflies and the more archaic representatives of existing types. For this purpose, I have chosen the wings of *Ameletus ornatus*, family Siphlonuridæ; not because I believe it to be the most archaic of existing types, but because it is archaic enough for our purpose, and happens to be the species on which most of the studies of larval wing-tracheation were carried out.

Comparing the wings of *Prottereisma* (text-figs. 1a, 3) with the fore-wing of *Ameletus* (text-figs. 1b, 4), the first thing we notice is the change in the general shape of the wing. That of *Prottereisma* is of the archaic elongate oval form seen in most of the Palaeodictyoptera and in the fore-wings of Perlaria, in which no definite tornus and termen are developed, but only a single continuously curved posterior margin from base to apex. In most recent Mayflies, *Ameletus* included, a definite *tornus* (*tu*) is to be recognised; the angle of the tornus divides the original posterior margin into a shorter basal part, to which the term *posterior margin* is still applied (called the *dorsum* in Lepidoptera, but the term is inapplicable to Mayflies, which do not fold their wings over their body in a roof-like manner), and a much longer distal part, called the *termen* or *distal margin*. The result of this is that the wing is now no longer of the primitive elongate oval shape, but

definitely triangular, the three angles being the base, the apex, and the tornus. In the evolution of this shape of wing there is a definite reduction of the areas served by the cubitus and anal veins, and a definite increase in the area served by the media and radial sector. Consequently, if Comstock and Needham's theory of interpolated veins is justified, we should certainly expect to find a number of them developed along the termen in *Ameletus*. At first sight, this appears to have happened, since we can find at once no less than five long veins, viz.  $2R_{2a}$ ,  $4R_{2a}$ ,  $R_{2b}$ ,  $R_{4b}$ , and  $M_2$ , which are not connected basally with their adjacent main veins. On the evidence of recent Mayflies alone, Needham's conclusions were perhaps warranted. But when we come to compare the venation of *Ameletus* with the fossil *Prottereisma*, we find that every one of these veins corresponds exactly with a true branch of a main vein present in the fossil; and, further, the total number of veins present in *Ameletus*, and their alternate convexity and concavity, agrees exactly with the conditions in *Prottereisma*. I have therefore no hesitation in assigning to the veins in the fore-wing of *Ameletus* the same names as I have already given to their homologues in *Prottereisma*.

In the section dealing with larval wing-tracheation, it will be shown that disconnection of the base of any branch vein is correlated with loss of its precedent trachea in the larval wing, and may well be a direct result of this larval condition.

By comparing the wings of *Ameletus* and *Prottereisma*, we are now able to see that the lengthening of the termen has taken place chiefly in the region served by  $R_{4+5}$  and  $M$ , the branches of these veins standing considerably further apart in *Ameletus* than in the fossil, whereas the area served by  $R_{2+3}$  has altered very little.

Turning our attention to  $Cu_1$ , we note that this remains a strongly convex vein, but its original triadic system of branching has been changed to a simple pectinate series, though the number of branches, seven in all, remains the same, the branches still being alternately convex and concave. Though superficially striking, this change is really a very slight one, consisting only of a movement basad, on to the main stem, of the triad called  $Cu_{1e}$  in text-figs. 1a, 3.

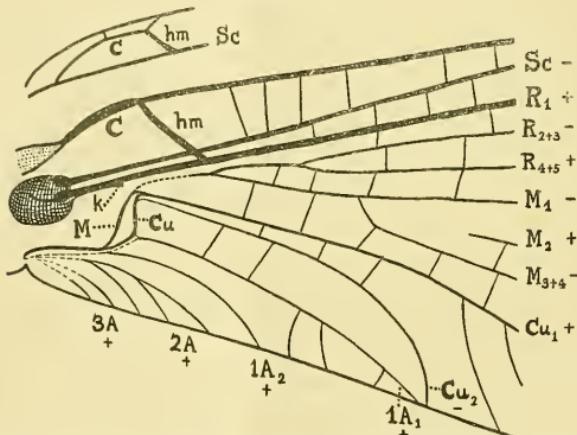
The greatest changes that have taken place in the evolution of the existing type of Mayfly wing are those in the basal region of the wing. For these, we must refer to the enlarged basal area of *Ameletus* shown in text-fig. 4, and this must be compared with the basal portion of the wing of *Prottereisma* in text-fig. 3. Here we note the following changes:—

(1) The separate costal vein  $C$  of the fossil has become fused with the costal margin, forming a thickened basal margin; only its posterior distal branch,  $hm$ , remains free, and forms the strong oblique brace,  $hm$ , in *Ameletus* and all recent Mayflies. The intermediate stage in this evolutionary process is well seen in the Jurassic Mayflies, the condition in *Mesephemera cellulosa* (Hagen) being shown in text-fig. 4, upper figure.

(2) M has become fused basally for a short distance with Rs, the basal stem of the two veins becoming obsolescent, but actually showing a weak connection with M only, while the lost origin of Rs is shown by a very definite stump projecting from  $R_1$  close to the base. In some recent Mayflies, however, Rs remains separate from M, and is attached tangentially to  $R_1$  just beneath hm. Both conditions may be regarded as specialisations involving the abortion of the original basal piece of Rs.

(3) The basal portions of M and Cu, before the first forkings of these veins, run close together as in *Prottereisma*, but both of them turn upwards almost transversely across the wing. At the upper end of this bent portion is the formation which I have called the cubito-median Y-vein, so greatly

TEXT-FIG. 4.



Basal portion of fore-wing of *Ameletus ornatus* (Eaton), Recent, considerably enlarged to show details of venation. k, stump of Rs. Above, costal vein and humeral brace (hm) in *Mesephemera cellulosa* (Hagen), Upper Jurassic of Solenhofen. For lettering, see p. 162.

reduced from its original conditions (as seen in *Prottereisma*) that it can only just be made out in text-fig. 4. At this point, Cu forks, and its two branches turn at right angles to its former course and run outwards about parallel to the posterior border of the wing.  $Cu_2$  remains, as in the fossil, a strongly-curved vein concave to the posterior border; but the shortening of its length has brought with it a definite increase of curvature, so that the weak sigmoid curve which this vein shows in *Prottereisma* becomes replaced by a single strong arch, concave to the posterior border. Other recent Mayflies, such as *Ephemera*, have the original sigmoid curve intensified, but the vein itself greatly reduced in length, and the clavus almost completely obliterated.

(4) The anal area, or clavus, in greatly reduced size, being about one-fifth of the total wing-length in *Ameletus*, as compared with about one-third in *Prottereisma*. The number of branches of the anal veins are correspondingly reduced, those of 1A to two definite branches, while 2A and 3A are only indicated by short, weakly-formed veins, as shown in text-fig. 4.

(5) The articulation of the wing, situated at the origin of Sc and R, becomes greatly strengthened by the formation of a hugh ovoid callus (text-fig. 4). It appears to be the growth of this callus which has forced the basal portions of M and Cu below it into their peculiar curved positions. In some recent Mayflies of higher type than *Ameletus*, these curved basal parts of M and Cu become strengthened and partially fused together; uniting with the bases of the anal vein also, they form an upwardly-curving arch convex to the posterior border, from which all the branches of Cu and A take their rise.

We thus see that, in the archaic family Siphluridae, as represented by *Ameletus*, the correspondence with the Lower Permian fossil Mayflies is exceedingly close, and the homologies of the veins perfectly clear. This, of course, refers to the fore-wing only. The hind-wing, which has undergone great reduction since Jurassic times, will be dealt with after the tracheation of the larval fore-wing has been considered.

#### TRACHEATION OF THE LARVAL WINGS.

The study of the tracheation of the larval wings in New Zealand genera of the family Siphluridae was carried out chiefly, as already stated, in the Cass Biological Station. Some material was also obtained around Wellington during my stay with Mr. Harold Hamilton, of the Dominion Museum, and the dissections of these were carried out at his home in Karori. I wish here to thank Prof. Chilton and Mr. Hamilton for the facilities they afforded me for carrying out this work.

The material studied consisted of numerous larvae of the following species:—*Oniscigaster distans* Eaton, *Coloburiscus humeralis* (Walk.), *Ameletus ornatus* (Eaton), and *Ameletus percitus* Eaton. The larvae of the first and last of these were very abundant at Cass, and provided the bulk of the dissections. The number of instars is not known for any of these larvae, but the wing-sheaths can be dissected out for at least five instars, showing comparative stages of growth from a tiny triangular bud up to a considerably elongated flap. For comparative purposes, I have designated the youngest of these last five instars as the *n*th instar, viz. that in which the wing-buds are very small flaps, capable of being dissected off with very fine scissors if great care is exercised. The following instars will be termed the (*n*+1)th, (*n*+2)th, (*n*+3)th, (*n*+4)th respectively, the (*n*+4)th being the last larval instar. In order to avoid too many figures, I shall give

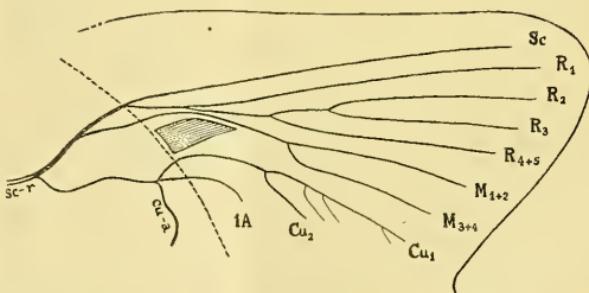
here only a series of drawings which I made from the wing-sheaths of *Ameletus ornatus*, a larva which has fairly transparent wings, is easy to dissect, and in which the tracheæ can be followed without any trouble. Characters in which the other larvae differed from this will be noted below.

The first point to be noticed is that the larval wing, in this Order, is soldered to the thorax over a considerable portion of its basal area.

The free distal portion of the wing is that which lies to the right of the dotted line in text-figs. 5-9. Great care is necessary, in dissection, to remove sufficient of the soldered basal part to ensure that the bases of the wing-tracheæ, and their connections, are not severed or damaged in the operation.

Just distad of the middle of the line marking the junction of the flap of the wing with the thorax, there is always present a somewhat triangular patch of hard chitin, shown shaded in all the figures. It at first separates the subcosto-radial group of tracheæ, including M, from the cubito-anal group, as shown in text-fig. 5 for the *n*th instar. But, in the next instar, it

TEXT-FIG. 5.

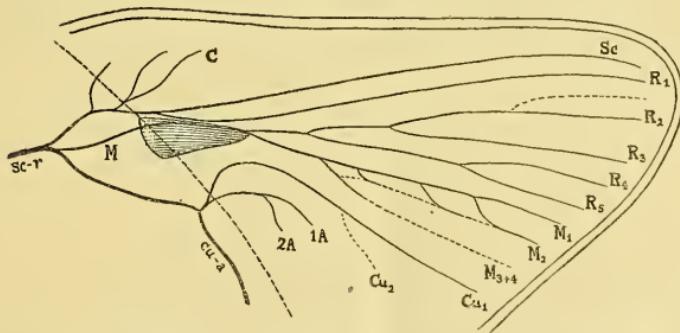


*Ameletus ornatus* (Eaton). Tracheation of fore-wing in *n*th larval instar.  
For lettering, see p. 162. ( $\times 97$ .)

moves forward a little, so as to overlie part of the base of M; and finally, in the last two instars, it comes to overlie the wholly or partially fused bases of R and M. From its final position in the last instar, it seems to me that this hard piece of chitin represents the large callus of the imaginal wing; its position in relation to the thorax is probably constant, its apparent movement forward being probably due to changes in the actual positions of the wing-tracheæ. The chief point of interest appears to me to be that it certainly does cause trachea M to run closer up to R than it naturally would if this callus were absent. Consequently, it may well be one of the factors which helped to bring about the fusion of M with Rs basally, as we find it in the majority of larval wings in the last four instars (text-figs. 6-8).

Text-fig. 5 shows a typical fore-wing of *Ameletus ornatus* in the  $n$ th larval instar. There is no costal trachea visible. The alar trunk connecting the subcosto-radial with the cubito-anal group of tracheæ is complete, though of small calibre, and the two groups are widely separated. Instead of coming off separately from the alar trunk, the tracheæ Sc, R, and M arise as separate branches from a single trachea of large calibre. Rs branches, as a simple triad, into  $R_2$ ,  $R_3$ , and  $R_{4+5}$ . Trachea M arches gently in front of the callus already mentioned, and thus comes very close up to Rs just where it comes off from  $R_1$ . Most of the larvae examined in this instar show exactly the condition given in text-fig. 5; but I found one larva in which trachea M had already captured trachea Rs at its base. This condition becomes the usual one in the following instars. M is only two-branched, as in the Order Perlaria. The tracheæ of the cubito-anal group are very fine in calibre; but I could distinctly make out  $Cu_1$  and 1A in all the larvae examined, and could see  $Cu_2$  in most of them. In following instars, no trachea is usually visible in  $Cu_2$ , though I found it quite well developed in a fine larval wing of the penultimate or  $(n+3)$ th instar shown in text-fig. 8.

TEXT-FIG. 6.



*Ameletus ornatus* (Eaton).—Tracheation of fore-wing in  $(n+1)$ th larval instar.

For lettering, see p. 162. ( $\times 87$ .)

Passing on to the next, or  $(n+1)$ th instar (text-fig. 6), we note that the callus has now come to overlie the base of M, and in the great majority of wings examined, trachea M has captured trachea Rs at its point of nearest approach basally. I have notes of a few exceptions, chiefly in the genus *Oniscigaster*, in which, both in this and the following instars, any of the following conditions may happen to occur:—

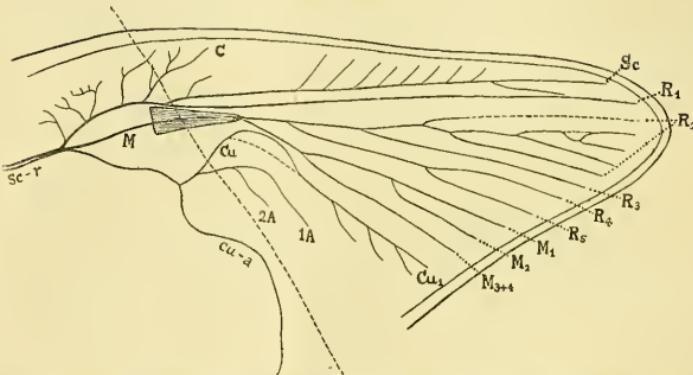
- (1) Tracheæ Sc, R, Rs, and M all come off in a bunch as separate tracheæ from a single point on the alar trunk.
- (2) R arises from Sc, but Rs and M arise close together from a point on the alar trunk a little below them.

(3) Rs and M are slightly separated basally, but come together so as to be almost indistinguishable while passing the callus, and then separate distally.

(4) Sc arises by itself from the alar trunk; considerably further down, a group of three separate tracheæ, R<sub>1</sub>, Rs, and M, arise close together.

All the above conditions are occasional variants only from the dominant condition, which is that shown in text-fig. 6. It should be noted that trachea M, in this instar, usually arises quite separately from trachea Sc + R<sub>1</sub>, and its course basally from alar trunk to callus diverges widely from that of the latter. The number of tracheæ developed from Rs is increased to four by the forking of R<sub>4+5</sub>, and there is an indication of the addition of an anterior branch to R<sub>2</sub> in the form of a pale band, which never, at any time, as far as I could see, develops more than the merest basal rudiment of a trachea, and usually possesses none at all. The number of branches of M

TEXT-FIG. 7.



*Ameletus ornatus* (Eaton). Tracheation of fore-wing in ( $n+2$ )th or antepenultimate larval instar. For lettering, see p. 162. ( $\times 41$ .)

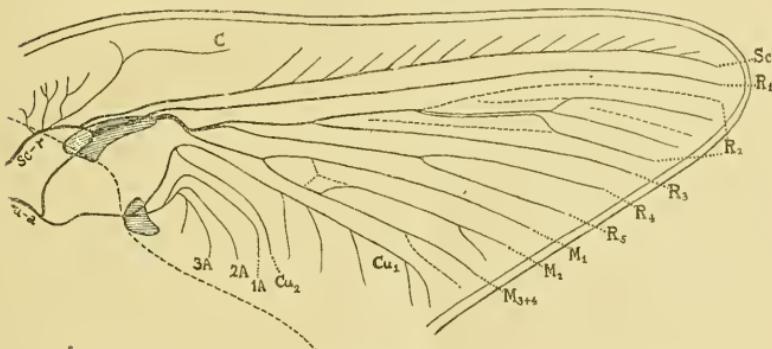
is also increased to three by formation of the triad M<sub>1</sub>, M<sub>2</sub>, M<sub>3+4</sub>; but the tracheal supply of the middle branch M<sub>2</sub> is quite irregular, and varies greatly in the different larvae examined. A separate costal trachea appears as a short basal anterior branch from Sc. The alar trunk continues complete, and of fair calibre.

Passing next to the ( $n+2$ )th or antepenultimate instar (text-fig. 7), we find the conditions not very different from those indicated for the previous instar, except for the presence of additional branches of R<sub>2</sub>, which now number five in all, and the establishment of the triad M<sub>1</sub>, M<sub>2</sub>, M<sub>3+4</sub> on a firm basis, with a single trachea supplying M<sub>2</sub> as shown. In text-fig. 7, I show a curious condition of trachea Cu<sub>1</sub> near the base. The course of the vein Cu<sub>1</sub> is indicated by the dotted line, but the trachea arches up out of its normal course, and passes close under M. I have seen this condition several times,

not only with  $Cu_1$ , but in other parts of the larval wing. It seems to indicate a certain amount of instability in the tracheation, and may possibly be the stage precedent to a more complete breaking down of the tracheal supply, as exhibited in many of the forms studied by Miss Morgan.

Text-fig. 8 shows the tracheation of the fore-wing in the  $(n+3)$ th or penultimate instar. In this stage, R, Rs, and M generally appear to arise as a single thickened trachea from the alar trunk, at a point somewhat removed from the origin of Sc, and beneath the callus. By careful manipulation, this apparently single trachea can be separated into its component parts, when it will be seen that it is in reality three separate tracheæ arising from almost the same point. In some specimens, however,  $R_1$  may still be found arising as a branch of Sc, while Rs and M arise as a single trachea well below it. I think the varying conditions seen in the later

TEXT-FIG. 8.



*Ameletus ornatus* (Eaton). Tracheation of fore-wing in  $(n+3)$ th or penultimate larval instar. For lettering, see p. 162. ( $\times 48$ .)

instars are almost wholly due to the presence of the callus, one or more of the original tracheæ taking a devious course to avoid passing under it, or possibly becoming displaced at ecdysis by the pressure of the harder mass of chitin.

In this instar, the number of branches of  $R_2$  is still five, and the most anterior of these never has any tracheal supply except a mere rudiment. Various irregularities may be noted. In the specimen figured, the trachea which usually supplies the most posterior branch of  $R_2$  arises alongside the trachea belonging to the branch above, and runs with it to about half its length, when it turns downwards and supplies the course of the most posterior branch for its distal half only. The trachea supplying  $M_2$  sometimes arises from  $M_{3+4}$ .  $Cu_2$  possesses a complete trachea in this specimen; but in the majority of wings examined, it either has no trachea or a mere rudiment. These are all individual variations in the tracheation, and

are of no significance except to indicate the essential variability of the tracheation in many of its details.

In this instar, the line of fusion of the wing-sheath with the thorax ceases to be straight, and shows a definite convex bulging between the subcosto-radial and cubito-anal groups of tracheæ. The alar trunk is still complete, but thrown into a strong loop. The large anterior callus already noted in previous instars now appears in close contact with the axillary area of the thorax, this position corresponding with that in the imaginal wing, where the callus articulates with the axillary process of the thorax. A new structure is apparent in the cubito-anal region, viz. a smaller, somewhat reniform, posterior thickened patch, shown shaded in text-fig. 8. This corresponds with the opaque and somewhat thickened anal area at the base of the imaginal wing; but it never becomes a true callus, *i.e.* it does not articulate with an axillary process from the thorax.

The last or ( $n+4$ )th instar differs from the previous one in the much larger size of the wing-sheaths, the strong development of the anterior callus, the very clear indication of the whole of the imaginal venation, including all the cross-veins and veinlets, and the presence of all six branches of  $R_2$ . In this instar, the tracheation is not easy to follow, owing to the strong pigment bands of the imaginal venation overlying it. As the general tracheation scheme is closely similar to that of the previous instar, and the same individual variations are equally apparent, it has not appeared necessary to me to figure it. One point of interest needs to be mentioned, viz. that I only succeeded in finding the complete alar trunk in one specimen of *Oniscigaster distans*. In all the others examined, the basal portion  $cu-a$  was missing, and the single trachea which gives origin to  $Cn$  and the anal veins appeared to arise from the same trunk as the other tracheæ above it. This is exactly the condition shown in Miss Morgan's figures (1912, pls. 5-7). Thus it will be seen that, if she had studied other instars as well as the last, she would not have fallen into the error of failing to homologise correctly the cubital tracheæ and veins, which it is quite evident she has done.

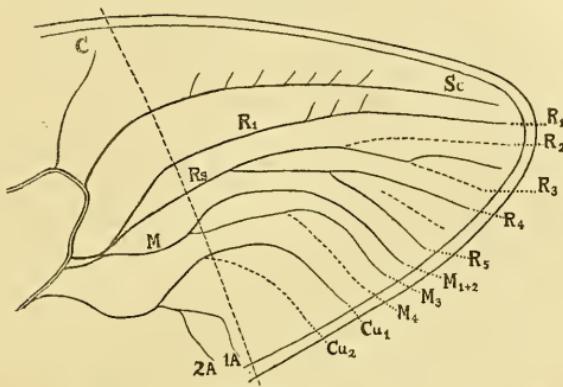
The above discussion applies to the fore-wing only. As the hind-wing is greatly reduced in size in all recent Mayflies, and differs very greatly from that of the Permian Mayflies, as well as from the fore-wing of recent forms, I have thought it best to summarise the evidence for its venational homologies in a separate section.

#### THE HIND-WING.

The dissection of the small hind wing-sheath of a Mayfly nymph is not easy, and I only succeeded in getting good preparations from the last two instars. Text-fig. 9 shows the tracheation in the hind-wing of *Amelitus ornatus*, penultimate instar. The alar trunk is complete, but there are no signs of a callus. The line of fusion with the thorax lies well out beyond the origins of the wing-tracheæ, as shown by the dotted line in the figure.

There is a separate costal trachea C, lying far above Sc; the latter trachea lies far above the group of R and M, which arise close together well down towards the cubito-anal group. Rs arises from R very close to the point

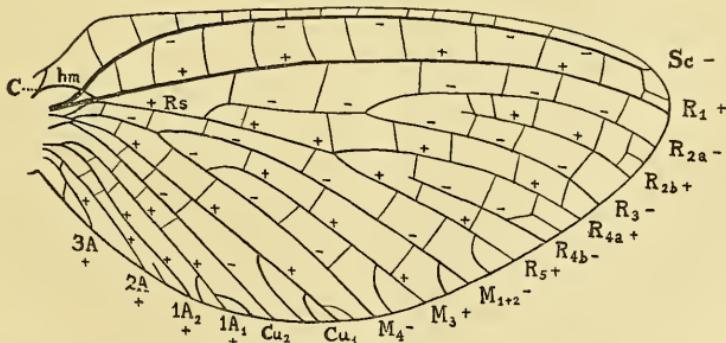
TEXT-FIG. 9.



*Ameletus ornatus* (Eaton). Tracheation of hind-wing in ( $n+3$ )th or penultimate larval instar. For lettering, see p. 162. ( $\times 87$ .)

where M curves slightly upwards, so as to come very close to it. Rs divides into two branches,  $R_{2+3}$  and  $R_{4+5}$ , each of which gives rise to a simple triad with incomplete tracheation. The middle branch of the triad of  $R_{2+3}$  is supplied by the trachea  $R_3$ , but  $R_2$  and the distal part of  $R_3$  have no tracheæ. The two outer branches of the triad of  $R_{4+5}$  have their tracheæ present, but

TEXT-FIG. 10.



*Ameletus ornatus* (Eaton). Venation of hind-wing. For lettering, see p. 162. ( $\times 16$ .)

the middle branch has none. M gives rise to a simple triad in which the trachea supplying  $M_{3+4}$  switches up into the middle branch distally, leaving the distal half of  $M_4$  without a trachea.  $Cu_2$  has no trachea.

In interpreting the above scheme, we must compare the imaginal venation shown in text-fig. 10 with the tracheation shown in text-fig. 9. There can then be no doubt as to the correct homologies of the main veins. Two points only are open to doubt. Firstly, what is the correct notation for the middle branch of the triad of  $R_{2+3}$ ? This appears to be a branch of  $R_3$ . But in the penultimate instar of *Oniscigaster distans*, I find the trachea  $R_2$  supplying this branch. I therefore conclude that the tracheation is variable, and give preference to the notation  $R_{2b}$  for this vein. This is done because, in the fore-wings of recent Mayflies, and also in both wings of the fossil *Protoreisma*,  $R_3$  is an unbranched vein. Secondly, what is the correct notation for the middle branch of the triad of  $M$ ? In this case, both in the larva of *Oniscigaster distans* and in the one figured, the trachea supplying it comes from  $M_{3+4}$ . In addition to this, the vein itself, in the imaginal wing, arises from  $M_{3+4}$  as a definite branch. All the evidence, then, points to the correct notation for this vein being  $M_3$ , the other members of the triad being  $M_{1+2}$  and  $M_4$ . In this respect, we must reckon that the hind-wings of *Ameletus* and *Oniscigaster* differ from their fore-wings, and also from both wings of *Protoreisma*. The explanation probably lies in a shifting, at some fairly early point in the evolution of the hind-wing, of the point of attachment of the middle member of the triad, followed at a slightly later time by the development of a corresponding new tracheal supply.

#### ALTERNATIVE INTERPRETATIONS.

Having now considered all the evidence available under the three headings already indicated, we may ask whether any of them offer any basis for an alternative interpretation. The answer to this must be, that, in the case of the evidence from Convex and Concave Veins, and from the Fossil Record, there can be no doubt whatever as to the true homologies of the veins, and no alternatives to the solution here given can be offered. In the case of the larval tracheation, we have noted a considerable amount of variation both in the branch tracheal supply and in the mode of origin of the main tracheæ from the alar trunk. To anyone, therefore, who pins his faith upon this kind of evidence alone, and who refuses to admit that offered under the two other headings, alternative solutions are possible. The two chief alternatives, of course, are those given in the table on p. 145 as the Comstock-Needham and Morgan notations respectively. We may ask whether the evidence from the tracheæ alone does really support either of these two schemes rather than the one we have given in this paper.

With regard to the original interpretation given by Comstock and Needham, this clearly assumed that there had been a basal fusion between  $Rs$ ,  $M$ , and  $Cu$ . The evidence of the tracheation certainly supports the idea of a basal fusion between  $Rs$  and  $M$ ; but it shows clearly enough that  $Cu$  remains quite distinct. It does not seem necessary to say more about this alternative

notation, for the simple reason that its authors themselves admitted that it was unsatisfactory ; and, later on, they accepted Miss Morgan's interpretation instead (see Comstock, 1918, chap. x.). We have, then, only to consider Miss Morgan's notation. With respect to this, we may note the following points:—

(1) The research was carried out on wings of the last larval instar only. In this instar the tracheation is the most variable of all, and the posterior continuation of the alar trunk is usually absent. In spite of this, Miss Morgan correctly interpreted the homologies of the cubital tracheæ, but failed, for some reason, to connect them with their true venational homologues in the imago. Had she examined the tracheation in this region in earlier instars, she could not have failed to note the close correspondence between the strongly bent cubitus in the larva and imago ; and her results, as far as the limits of Cu were concerned, would then have agreed with those given in this paper.

(2) The evidence for her chief innovation; viz. the crossing of a simple Rs over two branches of M, as in Anisopterous Dragonflies, is not forthcoming from the great majority of the larval wings examined, but only from the wings of a single species, in which, as she admits (*l. c. p. 98*), "half of the wing-pads showed the radial branching just described and half of them gave no sign of it." The species which gave, in only one-half of its representatives, an indication of Rs crossing over M, was a species of *Heptagenia*, a genus which is by no means the most archaic of the fifteen genera studied by Miss Morgan. Yet she accepts this evidence, against the weight of evidence supplied by all the other fifteen genera and the other species of *Heptagenia* included !

As I have already pointed out, new light on the venation of Dragonflies has made it certain that Rs does not cross over M in the Zygoptera, and has also rendered it extremely improbable that the trachea which does this in the Anisoptera is Rs at all. The evidence for a crossing of Rs over M in Mayflies to be found within the Order itself is, as we have seen, practically negligible. Thus Miss Morgan's whole case totters to the ground, and must be replaced by a more lasting structure.

To sum up, we have seen how the evidence from the Convexity and Concavity of Veins agrees absolutely with that offered by a study of the Permian fossil *Prottereisma*, and the combined evidence of these two lines of study is supported to a very great extent by that of the tracheation of larval wings, the only doubtful point in this latter evidence being its undoubtedly tendency to vary. Taken all together, the new system of homologies appears to me to be supported by so great a weight of evidence as to be at once acceptable in place of the hypotheses previously offered in the Comstock-Needham and Morgan notations respectively. At the same time it offers a new and clear basis on which to build up a system of classification within the

Order, which will present, to some extent at any rate, the real lines of evolution of the Mayflies through the long period of time from the Lower Permian to the present day. That problem may well be left to a later paper. I also hope to continue the series already begun on the venation of Odonata, and to show how, in that Order, the behaviour of the radial sector has followed the lines set out in this paper for the Mayflies, though very high specialisations of the Odonate venation have masked the original close similarity between it and that of Mayflies.

Cawthon Institute, Nelson,  
31 March, 1922.

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#### *Venational Notation used in the Text-figures.*

1 A, first analis ; 1 A<sub>1</sub>, 1 A<sub>2</sub>, its two branches. 2 A, second analis. 3 A, third analis. C, costal vein or trachea, separate from the costal margin. Cu, cubitus. Cu<sub>1</sub>, first cubitus ; Cu<sub>1a</sub>, Cu<sub>1b</sub>, Cu<sub>1c</sub>, its principal triad in *Prottereisma*. Cu<sub>2</sub>, second cubitus or vena dividens. cu-a, cubito-anal trunk trachea. cuf, primary cubital fork. hm, humeral brace, formed from the descending posterior branch of the costal vein. k, stump of Rs. M, media ; M<sub>1</sub>, M<sub>2</sub>, M<sub>3+4</sub>, the three branches of its triad. M<sub>5</sub>, its posterior branch, forming the upper arm of the cubito-median Y-vein, the lower arm being Cu<sub>1</sub>. M<sub>5</sub>+Cu<sub>1</sub>, in *Prottereisma*, the main stem of the cubito-median Y-vein, commonly called Cu<sub>1</sub>. mf, the primary median fork. Pe, precostal margin. R, radius ; R<sub>1</sub>, its main stem or anterior branch. Rs, radial sector ; R<sub>2+3</sub>, R<sub>4+5</sub>, its two main branches ; further branchings are indicated, first by the four veins R<sub>2</sub>, R<sub>3</sub>, R<sub>4</sub>, R<sub>5</sub>, then by the suffixes a (anterior) or b (posterior) attached to any of these four veins, and finally by numerical prefixes 1 to 5, to avoid further suffixes. Sc, subcosta. sc-r, subcosto-radial trunk trachea. tn, tornus.