

ON THE DEVELOPMENT OF THE WING-VENATION
IN ZYGOPTEROUS DRAGONFLIES, WITH SPECIAL
REFERENCE TO THE *CALOPTERYGIDÆ*.

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(Plates xxxii.-xxxiv., and Text-figs.1-6.)

In a previous paper concerning the development of the wing-venation in Dragonflies,* I dealt partly with the case of the *Zygoptera*. At that time, no larvæ of the family *Calopterygidae* were available for study. As this family undoubtedly includes the most archaic forms amongst the *Zygoptera*, it was clear that the solution of the problems still outstanding must be sought for within it. In indicating this in my former paper, I ventured the statement that "the many forms of *Calopterygid* larval wings will one day yield a wonderful harvest to the fortunate student who has a chance of investigating them." The *Calopterygidae* are, however, nearly all tropical forms. Even if a collector with the requisite knowledge could visit the places where they abound, there still remains the almost insuperable difficulty of photographing the wing-tracheæ in the recently-killed larva. The apparatus required for this purpose is too costly and too cumbersome to be taken on an expedition of this kind. The larvæ, too, require running water to live in, and do not take kindly to captivity. Hence they would not stand a long journey back to a base suitable for operations.

It seemed, therefore, that important problems awaiting solution might be indefinitely postponed unless some efforts were made to obtain at least those *Calopterygid* genera that were nearest to hand. In Australia, we have only one genus, *Diphle-*

* "On some Problems concerning the Development of the Wing-Venation of *Odonata*." These Proceedings, 1914, xxxix, Part i., pp.163-216, Plates xi.-xii.

bia. This enjoys the unique position of being the most *Agrionid*-like of all *Calopterygidae*. It is the most highly specialised genus of the subfamily *Epallaginae*. That subfamily is, however, the most archaic in the family. Hence, the phylogeny of *Diphlebia* is of such a nature as to offer good hopes for the solution of some of our problems. These solutions could not, in any case, be allowed to rest on evidence from a single genus, or from two or three closely related genera. Now the genus *Calopteryx*, which also—but in a direction quite different from that of *Diphlebia*—combines high specialisation with a number of archaic characters, is available in Europe. I, therefore, wrote last year to Dr. Ris, of Switzerland, urging him to do his utmost to secure larvæ of *Calopteryx* in the spring, with a view to photographing the tracheation of the larval wing. Meanwhile, I searched assiduously for the rare larva of *Diphlebia lestoides* Selys, of which I had previously found only one specimen in the course of nine years' collecting.

A further difficulty confronting us was the fact that the wing-cases of *Calopterygid* larvæ are tough, hairy, and opaque, offering very poor material for photographic work. Dr. Ris had already mentioned this to me as a point which had previously deterred him. I suggested to him that it would be necessary to secure larvæ that had just undergone ecdysis, so as to photograph them before the wings had had time to harden up and become opaque. My letter reached him in April, 1914. A few days later, he went to a known locality for *C. splendens* Harris, and was both surprised and delighted to find a number of larvæ exactly in the most suitable stage. The wing-tracheation of these specimens was photographed. I have to thank Dr. Ris for his kindness in offering me these beautiful photographs for use and publication in this paper (Plate xxxiv., figs. 1-3).

Meanwhile, the search for *Diphlebia* larvæ went on without result until September last. For their discovery, I am indebted to the kindness and energy of Mr. F. W. Carpenter, M.A., of Sydney Grammar School. While staying with me at Wentworth Falls, he kindly offered to make an exhaustive search of the rocks in Lilian's Bridge Creek—a locality which I had indicated

as likely to yield good results. As a result of two days' searching, six fine larvæ of *D. lestoides* were taken, clinging close to the undersides of rocks. Two were in the last instar, two in the penultimate, and two in the antepenultimate. One of the first was apparently approaching metamorphosis. I, therefore, killed it at once, and made camera-lucida drawings of the wing-cases. These drawings led to an interesting discovery, but were not reliable guides to the problems on hand. On my return home, a week later, the other larva in the last instar was so advanced that it had to be dealt with at once. The wing-cases were exceedingly hard and opaque, so that it was most difficult to obtain any photographic results of value. The results are shown in Pl. xxxiii., figs.1-2. Of the other four larvæ, one in each stage was dealt with at once. The wings were fairly hard, and yielded only moderately good results (Pl. xxxii., fig.3). The other two were kept alive, in the hope that they might undergo ecdysis. They both gradually grew weaker, but one managed just to survive an ecdysis, and yielded fairly good results (Pl. xxxii., figs.1-2: Pl. xxxiii., fig.1).

In the broad outlines of venation, the *Epallaginae* are more archaic than the *Calopteryginae*. I shall, therefore, deal with *Diphlebia* first, and then indicate the chief points in which *Calopteryx* either agrees with, or differs from it.

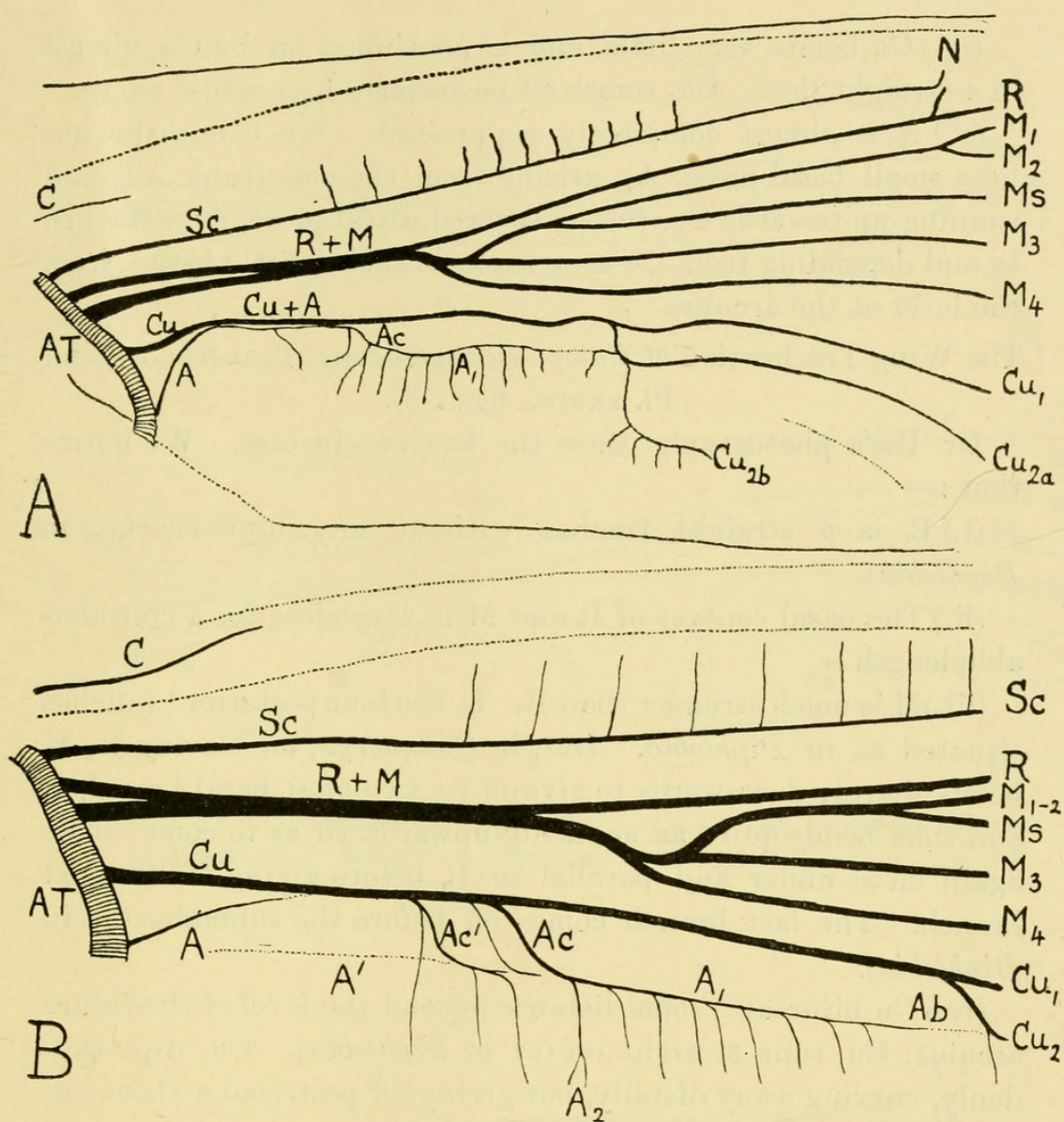
The Wing-Tracheation of *Diphlebia lestoides* (Text-figs.1-2; Pl. xxxii., figs.1-3; and Pl. xxxiii., fig.1).

The last three instars were studied, but only the antepenultimate and the penultimate showed the tracheation; the larvæ, in the last stage, had the tracheation masked by cuticularisation (see below). In both instars, the following results were noted—

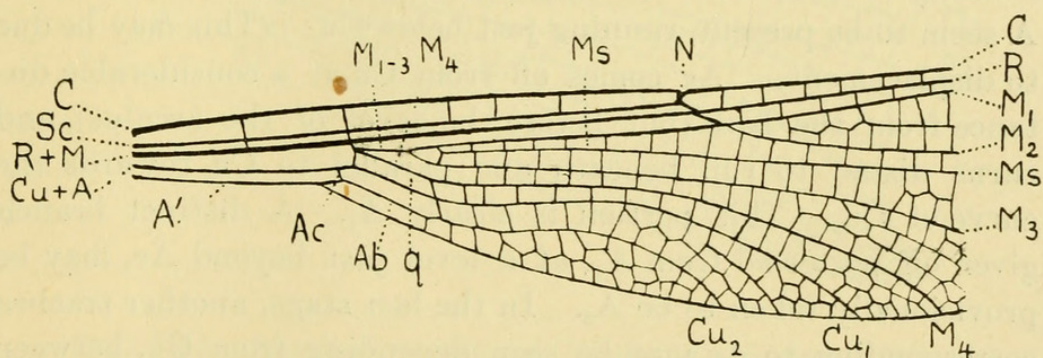
(i.) R is a straight trachea without a single branch. (The waviness in the photographs is due to unavoidable displacement in cutting off the wings).

(ii.) The basal contact between R and M is not very close.

(iii.) M is a stronger trachea than R, and gives off *four* posterior branches. Three of these come off close together near the level of the bifurcation of Cu. The fourth comes off under the subnodus (level of N in figures).



Text-fig. 1.—Tracheation of larval wing of *Diphlebia lestoides* Selys. A. Antepenultimate instar. B. Penultimate instar. Compare Pl. xxxii., figs. 1-3, Pl. xxxiii., fig. 1.



Text-fig. 2.—Imaginal venation of *Diphlebia lestoides* Selys, for comparison with Text-fig. 1.

(iv.) Cu bends very little, and is continued on by Cu₁ almost in a straight line. Cu₂ comes off posteriorly in a gentle curve.

(v.) A is almost completely suppressed. We can make out (a) a small basal piece, A₁, arising from the alar trunk AT, and running up towards Cu, (b) the severed distal piece, Ac, attached to and depending from Cu as a weak branch a little basal from the level of the arculus.

The Wing-Tracheation of *Calopteryx splendens* (Text-figs.3-4, and Pl. xxxiv., figs.1-3).

Dr. Ris's photographs show the last two instars. We notice that:—

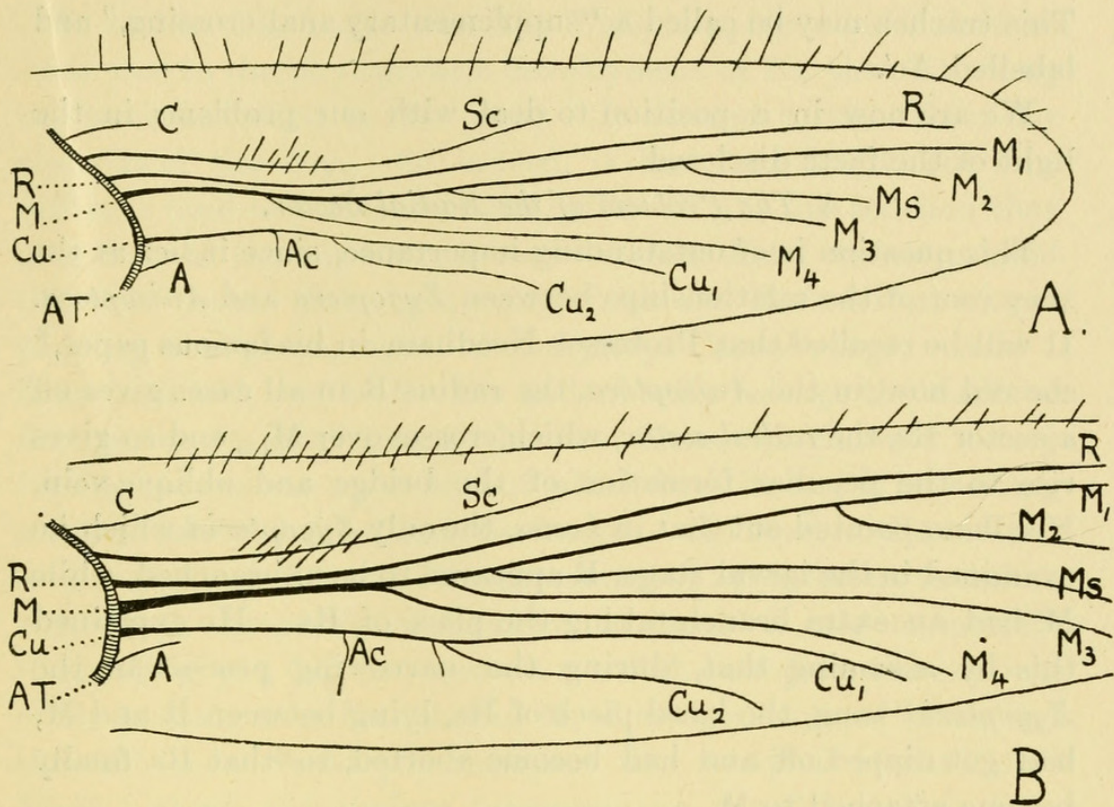
(i.) R is a straight trachea without any branches (as in *Diphlebia*).

(ii.) The basal contact of R and M is very close for a considerable length.

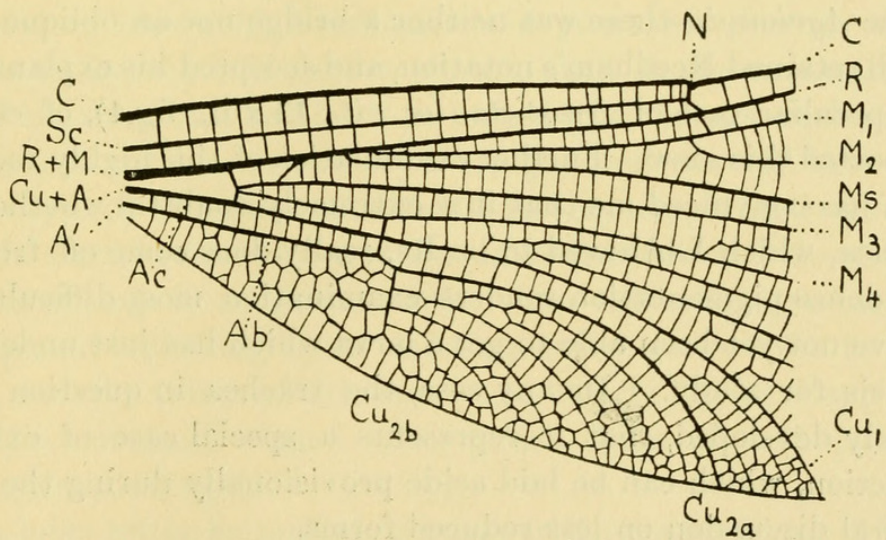
(iii.) M is much stronger than R. It has four posterior branches situated as in *Diphlebia*. But, in *Calopteryx*, on leaving R, M bends sharply downwards to give off its two most basal branches, and then bends quite as suddenly upwards so as to come to lie again close under and parallel to R before giving off its next branch. The last branch comes off before the subnodus (as in *Diphlebia*).

(iv.) Cu bifurcates some distance beyond the level of the future arculus; Cu₁ runs straight on (as in *Diphlebia*). Cu₂ dips suddenly, curving away distally, but giving off posteriad a short but distinct branch, Cu_{2b}.

(v.) A is distinctly seen arising from the alar trunk, AT, and running towards Cu. In the penultimate instar, fine strands of A seem to be present, running just below Cu. (This may be due to displacement). Ac comes off from Cu at a considerable distance from the base (but before the level of the arculus), and turns distad to run beneath and parallel to Cu towards the curve of Cu₂. This portion is clearly A₁. A distinct branch given off posteriad from A₁, at a level just beyond Ac, may be provisionally taken to be A₂. In the last stage, another trachea corresponding to Ac may be seen depending from Cu, between Ac and the base. This formation is, I believe, quite unique.



Text.fig.3.—Tracheation of larval wing of *Calopteryx splendens* Harris.
A. Penultimate instar. B. Last instar. Compare Pl.xxxiv., figs.2-3.



Text-fig.4.—Imaginal venation of *Calopteryx splendens* Harris, for comparison with Text-fig.3.

This trachea may be called a "supplementary anal crossing," and labelled Ac' .

We are now in a position to deal with our problems in the light of the facts disclosed.

A. *The Problem of the Radial Sector.*

This question is of outstanding importance, since it lies at the very root of the relationships between *Zygoptera* and *Anisoptera*. It will be recalled that Professor Needham, in his famous paper,* showed how, in the *Anisoptera*, the radius R in all cases gives off a sector Rs , the *radial sector*, which crosses over $M_{1,2}$, and so gives rise to the peculiar formation of the bridge and oblique-vein. Needham pointed out that in *Lestes*, the only *Zygopterid* which he examined in the larval stage, R appeared to be unbranched, while M had an extra branch taking the place of Rs . He explained this by assuming that, during the narrowing process in the *Zygopterid* wing, the basal piece of Rs , lying between R and M , had got nipped off and had become aborted, so that Rs finally became attached to M .

Now this explanation has been tacitly accepted by all students of *Odonata*, including Dr. Ris and myself, for a good many years. Even when, on the completion of my last paper on this subject (*loc. cit.*), I was faced with the fact that, in all the *Lestidæ* and *Agrionidæ* examined by me, R was always unbranched, and that in the *Agrionidæ* there was neither a bridge nor an oblique vein, I still retained Needham's notation, and accepted his explanation. The peculiar case of *Neosticta* (*loc. cit.*, Pl.xiii., fig.4), of course, supported this view. Further examination of this highly reduced form has convinced me that it is extremely doubtful whether the trachea, which I believed to be Rs , really does come off from R . The dense pigmentation renders examination most difficult, and I have not yet been able to get a larva which has just undergone ecdysis for study. In any case, the trachea in question is so weakly developed, that it represents a special case of extreme reduction, which can be laid aside provisionally during the more general discussion on less reduced forms.

* "A Genealogic Study of Dragonfly Wing-venation." Proc. U. S. Nat. Mus., xxvi., 1903, pp.703-764, Plates xxxi.-liv.

It was in the hopes that the *Calopterygidae* would show us some clue to the phylogenetic development of Rs, that I took up the work embodied in this paper. It seemed certain that they alone held the key. So, indeed, it has turned out, but how different (and how much simpler, after all!) is the solution they give us from the one we expected. I feel that I cannot present the case better than by quoting from Dr. Ris's letter, accompanying the photographs of *Calopteryx* larval-wings. And I must here add, that to Dr. Ris undoubtedly belongs the credit of first seriously entertaining the new ideas, which were slowly forcing themselves upon us, but which both he and I, for so long a time, remained unwilling to accept. He says:—"Now what do you think of this troublesome matter of zygopterous venation, with those ontogenetic documents in hand? I said to myself: 'Supposing you did not know a word of anisopterous venation, of Rs crossing over branches of M, of bridges, oblique veins, and the rest—how would you interpret this nymphal tracheation'? Well, I think the obvious interpretation would be—Vein R in this wing is *unbranched*; all the sectors are branches of the media M! With comparatively little modification (shifting of second and third branches of M—numbered from base—distad) of this scheme, you arrive at what is shown in the *Agrionidae*. And still, with not *very great* modification, you arrive at *Lestes* and *Synlestes*, as shown by Needham's and your own photos.; shift the second branch still further distad, until it becomes a tributary of the third one, and let it be united (for obvious mechanical reasons!) to the main branch by a bridge—and you will have the *Lestine* type of venation. All this is so very simple (and ruinous to my favourite construction of November last!) that I do refrain from accepting it as given truth. Can there be anywhere in development a shifting of an existing radial sector over to the media, and the traces of this fact be so utterly lost as it appears from the examined wings? Now please think of that matter, and let me know again!"

In a later letter he replied to some criticisms of mine: "You know, I am hesitating in interpretation of *Zygopterous* veins; old views are shaken; new ones not yet fully established; my

opinion regarding the unbranched radius is tentative; I am ready to give it up at any serious evidence for the contrary."

Finally, after studying the photographs of the wings of *Diphlebia* which I sent him, and which I pointed out were conclusively in favour of the new theory, he wrote: "I now think that the Unbranched Radius Theory will win the day."

I may add that the study of *Diphlebia* and *Calopteryx* at once convinced me that we had to deal, in the *Zygoptera*, with an originally unbranched radius, which has remained unbranched right down to the present day. We may summarise the evidence for this under three headings, as follows:—

1. *Direct Evidence from the Larval Wings.*

In every *Zygopterid* larval wing so far examined* (and these by now amount to a considerable number of genera), R is unbranched, and M has one branch more than in the *Anisoptera*. The differences between *Calopterygidae*, *Agrionidae*, and *Lestidae* are distinct, but of a lower order of significance. They may be stated thus:—

(a). *Calopterygidae*—M gives off three branches in rapid succession close to the arculus, and a fourth at the level of the subnodus.

(b). *Agrionidae*—M gives off one branch at the arculus, two more at about the level of the subnodus, (one usually exactly below it), and a fourth placed more or less distad from the subnodus.

(c). *Lestidae*—M gives off two branches close to the arculus; the third and fourth come off distad from the subnodus by means of a common stem, which soon bifurcates. From the lower of these two branches, a long bridge is developed backwards towards the main stem of M.

2. *Ontogenetic Evidence.*

We know the condition of R in the last *two* instars of *Calopteryx*, in the last *three* instars of *Diphlebia*, and in the last *four* stages of *Austrolestes*. Earlier than this, I have not been able to go, the tracheation being too feeble to deal with. In all of

* With the doubtful exception of the problematical *Neosticta*.

these, R is unbranched. As a contrast to this, in the *Anisoptera*, I find Rs present as a distinct sector in the very earliest stages of *Hemicordulia* and *Æschna* of which it is possible to obtain a photograph. Dr. Ris also finds it present in a very early stage of *Libellula depressa*, and Needham shows the same condition for all ontogenetic stages of *Gomphus descriptus*. Thus, the ontogenetic evidence points to an originally unbranched radius for all *Zygoptera*, and an originally branched radius for all *Anisoptera*.

3. Palæontological Evidence.

In the *Protodonata* (Upper Carboniferous and Permian), the family *Meganeuridæ* offers important evidence. The best-known species, *Meganeura monyi* Brongniart, has R *unbranched* in the hindwing, but with *two distinct branches* in the forewing. A smaller species, *Meganeurula selysi* Brong., has R *unbranched* in both wings. A Permian species, *Typus* (*Tupus*) *permianus* Sellards, has R *branched* in both wings, and shows clear evidence of having possessed the bridge and oblique vein of the *Anisoptera*. Thus, it is fair to conclude that, in the *Protodonata*, forms that were otherwise closely allied had a variable condition of the radius, which might be branched or unbranched in both wings, or branched in one wing and unbranched in the other.

In the *Odonata* of the Lias and Upper Jurassic, we find definite *Anisoptera* with the radius branched, the oblique vein and bridge present. We also find a few undoubted *Zygoptera* (*Calopterygidae*) with the radius unbranched. There remain the group which Handlirsch named *Anisozygoptera*, and which he claimed to be intermediate between true *Anisoptera* and *Zygoptera*. A careful examination of these forms shows:—

(a). That the *Heterophlebiinæ* have an unbranched radius, with a long bridge developed as in the *Synlestinæ*.

(b). That all the other forms have an unbranched radius and no bridge.

Intermediate forms, like *Meganeura monyi*, are not found in the Mesozoic strata. Every form so far known can be, therefore, definitely classed as *Anisopterous* or *Zygopterous*, according to the condition of its radius.

On the totality of the above evidence, which I consider to be very strong, a new view of the venation of *Zygoptera* seems to me to be not only indicated, but absolutely necessary. For this new view, which I now present for the first time, no better name than the "Unbranched Radius Theory" (the name given by Dr. Ris) can be found. We may enunciate the theory as follows.

The basic difference between *Anisoptera* and *Zygoptera* is the condition of the radius, a difference which is more radical than that of the presence or absence of the triangle, since it goes further back in point of geological time. In all *Anisoptera*, the radius has a single branch, the *radial sector* (Rs), which crosses two branches of the media ($M_{1,2}$); a short bridge is also developed in connection with it. In all *Zygoptera*, the radius is unbranched; a bridge is absent,* except in *Lestidæ*, when it is very long. In *Anisoptera*, the media (M) gives off only *three* posterior branches, so that Rs lies between the second and third, counting from the base. In *Zygoptera*, the media gives off *four* posterior branches, one of which takes the place of Rs, *i.e.*, supplies (in the larval wing) the area lying between the second and what is here the fourth branch of M, counting from the base.

In the *Protodonata*, the condition of the radius was variable, and of no greater than generic value. Fixation of the condition was most probably correlated with the formation of arculus, nodus, and pterostigma, which began in the Permian. Difference in wing-breadth may have been the original determinant whether Rs was to be present or not. In any case, intermediate forms died out before the Lias was reached. We there find the *Odonata* represented by a race of robust forms—the *Anisoptera*—with the radial sector present, and the discoidal cell divided into triangle + supertriangle; and by a race of slenderer forms (many of them still of large size)—the *Zygoptera*—with the radial sector absent, and the discoidal cell not definitely divided.

The development of the three main types of *Zygopterid* wing-venation may be shown thus:—A glance at Fig.3,A,B, shows that, on the ontogenetic evidence, the *Calopterygidae* have tended

* There may be a *very short* bridge in *Rhinocypha* and *Chalcopteryx*, but the larvæ are not available for examination.

to move the three most basal branches of M closer together. Thus the *Calopterygidae* and *Agrionidae* have a common origin in forms in which these three branches lay further apart than in recent *Calopterygidae*, but not so far apart as in recent *Agrionidae*. The reduction of the prenodal area in the latter family is clearly correlated with the extended condition of the medial branches. For, obviously, three branches are not needed to support so short a prenodal area. As regards the *Lestidae*, I find that the most distal branches of M arise by a common stem in all the last four instars of *Austrolestes*, and in all instars of *Synlestes* (three) that I have examined. Thus, I conclude that this is a primitive condition, probably independently inherited, and not brought about (as Dr. Ris suggested) by the movement distad of one branch so as to become a "tributary" of the other. Support for this view is forthcoming in the fact that the Liassic *Heterophlebia* shows this condition fully formed, as in our recent *Synlestes*. The same fossil supports the view that, in *Lestidae*, when the prenodal area became reduced, the second branch of the media (counting from the base) travelled basad away from the nodus, and took up a position similar to that seen in *Calopterygidae*. If that be so, this particular character was independently evolved in these two families, and cannot serve to indicate a close relationship between them. The totality of evidence tends to bring the *Calopterygidae* and *Agrionidae* close together (the common character of the *absence of a long bridge* is very important), and to separate the *Lestidae* out as a very distinct group of independent origin.

In now definitely rejecting Needham's explanation concerning the shifting of Rs over to M, I must lay the greatest stress on the ontogenetic evidence. If such a change as Needham pictured had ever taken place, *it is almost inconceivable that not the slightest record of it should now be left in the ontogenetic stages of the larval wing*. On the other hand, if such evidence can be found, the new theory must give way to Needham's original supposition, or some other theory in accord with the ontogenetic evidence.

If we now accept the Theory of the Unbranched Radius, four main consequences arise :—

(i.). Handlirsch's Suborder *Anisozygoptera* becomes untenable, and must be merged into the *Zygoptera*. The *Heterophlebiinae* become *Lestidae*, all the rest of the forms *Calopterygidae*.

(ii.). The crossing of Rs over M_{1+2} is no longer a character separating the *Odonata* from all known insects, but only separates the *Anisoptera* from the *Zygoptera*.

(iii.). The dichotomy between *Anisoptera* and *Zygoptera* becomes far more pronounced than heretofore. Consequently, the possibility of finding such structures as, for instance, reduced rectal gills in *Calopterygidae*, must be regarded not only as very remote, but, if the theory is strictly true, they should not be expected to occur at all.

(iv.). A name and a notation are required for the extra branch of the media in *Zygoptera*. Counting the distal end of the main stem, there are five separate branches of the media. We cannot name these M_1 , M_2 , etc., to M_5 without destroying the obvious homologies of M_4 and M_2 in the *Anisoptera* with the most basal and most distal branches of M respectively in the *Zygoptera*. A name that would suggest the analogy of the extra branch with Rs in the *Anisoptera* would be the most suitable. I, therefore, propose the special term *Zygopterid Sector*, with the notation M_s . This notation is clearly the most suitable one, since it allows of the preservation of the homologies of the other branches, and suggests the analogy with Rs which this sector undoubtedly possesses. It is adopted in the figures accompanying this paper.

As it is of all things the most necessary, both for systematic and biological workers, that the notation for *Odonate* wing-venation should be speedily and finally settled, the new departure, here instituted, should be criticised at once, and any possible evidence against the new theory should be immediately brought forward. We do not desire change for the sake of change. But we refuse to remain bound to a notation which is clearly both incorrect and misleading, such as the use of Rs in *Zygoptera* when there is no Rs. In this connection, those who have the opportunity of examining the larval wings of other *Zygopterid* (and particularly *Calopterygid*) genera should do so at once, to see whether they add weight to the new theory or disprove it.

In North America, the study of all possible ontogenetic stages of *Hetaerina* and *Archilestes* would be of great value.

B. *The Problem of the Anal Vein.*

In my previous paper (*loc. cit.*), I showed that the anal vein of imaginal *Odonata* was secondarily developed by a backward growth from Ac, and I named it the "secondary anal vein," A'. Dr. Calvert (*in litt.*) objects to the term "secondary," and suggests "recurrent" as a better term. I am quite willing to accept his suggestion, though I fail to see the objection to the term "secondary." A glance at Fig. 6 shows how this vein can be actually seen developing backwards in *Diphlebia*, during larval cuticularisation. In any case, A' remains as the notation for this vein.

As regards the "anal bridge," Ab, Mr. Herbert Campion tells me that Dr. Ris has already employed (apart from tracheational studies) the notation A* for this vein. Dr. Ris's notation should take priority over mine, but for the fact that the use of the asterisk in notation is an innovation much to be deplored, and, as a matter of fact, "preoccupied" by the general consent and use of centuries. A* in any printed work (including scientific publications) means "A (see reference below)." To illustrate the impossibility of accepting such a notation, I need only remark that the next author who wanted to use it, and at the same time to refer the reader to the place where Dr. Ris originated it, would have to print the absurdity A** (unless he were lucky enough to get A*†!). Surely such signs as *, †, ||, need not be dragged into our notation at all. They should all be considered preoccupied, by general consent. Concerning the structure of Ab in the *Calopterygidae*, we see (Figs. 2, 3B, 4) that it really is formed along A₁ in the older forms, as I previously stated. In *Anisoptera*, A₁ reaches Cu₂; in *Calopterygidae*, it just fails to do so; in *Agrionidae* and *Lestidae*, only a remnant of A₁ is left. We may, therefore, fairly retain Ab as a unit in the *Zygoptera*, and define it as "the vein which runs from the posterior end of Ac up to Cu₂."

There remains the curious formation Ac' in *Calopteryx* (Fig. 3B). This seems to be introduced simply because, in the larva, Ac lies

some distance from the base, and there is a wide anal wing-space left between it and the base without tracheal supply. In the imago, it seems to be represented by the *first* cubito-anal cross-vein, Ac being the *third*, which is often seen to be slightly oblique (Fig.4).

C. *Supplementary Bridges in Calopterygidae.*

In *Diphlebia*, and probably also in *Philoganga*, the long supplement, lying between M_1 and M_2 , is fed by a trachea which drops from M_1 , and supplies weak distal and proximal branches to the developing supplement. In the imago, this condition is reproduced by an oblique vein, representing the stem of the descending trachea, and a short "bridge," which is, in reality, only the proximal portion of the supplement. Anyone who will examine the formation of Mspl and Rspl in *Anisoptera*, particularly in *Æschninae*, will see a similar method of tracheal supply carried to excess. In *Æschna brevistyla*, I have sometimes seen as many as *three* depending tracheæ, all supplying the supplement. As, however, they are all of more than one cell's length, they do not get mistaken for "oblique veins" in the imago. But they are homologous with the latter, and the proximal parts of the supplements are the homologues of "bridge-veins."

A similar short "bridge-formation" is observable (apparently) extending Ms very slightly proximad in *Chalcopteryx* and *Rhincocypha*. This simply shows us that, in the *Calopterygidae*, the wing required extra support in the region just distal from the arculus. In some forms, Ms did not arise sufficiently close to M_3 to give the necessary support, so a short "bridge" was developed to supply the deficiency. In others (*Calopteryginae*), extra support was gained by a fusion with the radius.

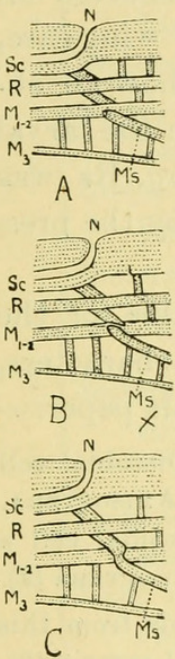
Thus we see that short "bridges" and "oblique veins" may be developed in connection with almost any sector or supplement which requires strengthening basally. The "bridge" of *Anisoptera* and the "long bridge" of *Lestidae* are the only two, out of probably very many attempts of this kind, which have attained real systematic importance, by attaining a definite structure and constancy throughout a whole group of genera.

D. Cuticularisation of the Larval Wing (Pl. xxxiii., figs.2-3;
Text-figs.5-6).

The wings of *Diphlebia* larvæ well advanced in the last instar show a condition not hitherto recorded in any works known to me., viz., a definite cuticularisation of the larval wing, outlining, but distinct from, the future venation of the imago. This condition caused me considerable trouble, since I found (in the larva examined at Wentworth Falls by camera-lucida drawings) what

appeared to be all stages in the development of a basal stem connecting M_s with R . At first, I believed that it was actually *trachea* M_s which was growing back on to R (how much the wish was father to the thought!). Dr. Ris, however, with characteristic insight, at once gave it as his opinion, on seeing the photographs taken from the second specimen, that here was a cuticularisation of the larval wing taking place, preparatory to the development of the imaginal venation within. This is clearly correct. We have all seen, of course, the pattern of the imaginal venation left behind on the larval wing-case in the exuviae, but I do not think the actual formation of this pattern, as apart from the formation of the true venation, has ever been noted or figured. A point of interest in this cuticularisation is that it seems to take place somewhat unevenly.

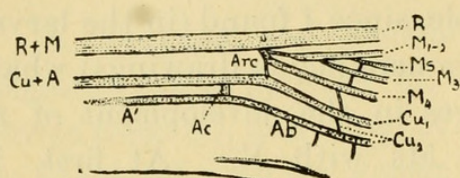
Thus in Pl. xxxiii., fig.3, we see the extreme base of $M_{1,3}$ still unaffected, the transparent trachea plainly showing through as a narrow stalk. The bases of M_3 and M_s have only a little cuticularisation. In the case of A' , in one of the Wentworth Falls specimens, the process of gradual backward growth was beautifully shown (Fig.6). Again, in the case of M_s , as the



Text-fig.5.*

* *Diphlebia lestoïdes* Selys. Last larval instar. To show progressive stages in the cuticularisation of M_s and its connection with R .—A, in right hindwing of first larva—B, in right forewing of first larva—C, in right forewing of second larva. (Camera-lucida drawings made from the under side of the wing-case). Compare Pl. xxxiii., fig.2.

cuticularisation gradually overspread the base of the trachea, it continued to grow out *under* the main stem of M, and finally became united with a strong, slanting cross-vein from R, below the subnodus, thus forming a veritable *radial sector* on the wing-case itself, though the trachea Ms remained attached to M. Three stages in this growth are shown in Fig.5. These were



Text-fig.6.*

drawn from the two Wentworth Falls larvæ in the last instar. It is important to note that the connection with R was effected on the *underside* of the wing-case, since this seems to show an ob-

vious difference of level between tracheæ R and M in the larval wing, and helps us to understand how, in *Anisoptera*, Rs was able to pass below M_{1-2} without becoming strangled by the pressure of these overlying tracheæ.

In conclusion, I offer an amended dichotomous table for the classification of the *Zygoptera*, based on venational characters, with particular reference to the points mentioned in this paper:—

- | | | | |
|----|---|--|-----------------------------|
| 1. | { | R once-branched. M with three posterior branches. Discoidal cell divided into triangle + supertriangle..... | Suborder ANISOPTERA. |
| | | R unbranched. M with four posterior branches. Discoidal cell a simple quadrilateral | Suborder ZYGOTERA (2). |
| 2. | { | Ms arising from M_2 ; a long bridge developed backwards from this point..... | Family LESTIDÆ (3). |
| | | Ms arising from the main stem of M. No long bridge | 4. |
| 3. | { | The long bridge runs back to meet M_{1-2} | 5. |
| | | The long bridge runs back to meet M_3 | 6. |
| 4. | { | M_3 and Ms close to arculus; M_2 at subnodus. More than two antenodals | Family CALOPTERYGIDÆ†(7). |
| | | M_2 and Ms close to subnodus (one of them usually directly under it), M_2 distally placed from subnodus. Normally two antenodals, rarely more (<i>Thaumatoneura</i> , fossils, and occasional anomalies)... | Family AGRIONIDÆ (8). |

* *Dipblebia lestoides* Selys. Last larval instar. To show method of cuticularisation of A' backwards from Ac towards base of wing. (Camera-lucida drawing.) Compare Pl. xxxiii., fig.3.

† Fossil forms of this family are omitted.

5. { Robust forms with many antenodals. Quadrilateral of hindwing much wider than that of forewing. Subfamily *Epiophlebiinae*.
Slender forms with two (rarely three) antenodals. Quadrilaterals of both wings narrow, with sharply acute distal angle. Subfamily *Lestinae*.
6. { Robust forms with many antenodals. Quadrilateral wide, irregular. (Extinct). Subfamily *Heterophlebiinae*.
Slender forms with two (rarely three) antenodals. Quadrilaterals of both wings narrow, with sharply acute distal angles. Subfamily *Synlestinae*.
7. { Sectors of the arculus attached to R. Hence, quadrilateral very wide basally. Subfamily *Thorinae*.
Sectors of the arculus not attached to R. 9.
8. { Nodus very close to wing-base, at about one-seventh of the total wing-length. Numerous postnodals. Subfamily *Pseudostigmatinae*.
Nodus at from one-fourth to less than one-half of the total wing-length. 10.
9. { Sectors of arculus arising at or a little above middle of arculus. No upward arching of M_{1-s}. Pterostigma normal. Subfamily *Epallaginae*.
Sectors of arculus arising below middle of arculus. M_{1-s} arched strongly up to re-fuse with R. Pterostigma false or absent. Subfamily *Calopteryginae*.
10. { Main veins diverging distally; intercalated sectors present besides the postnodal sector. Subfamily *Megapodagrioninae*.
Main veins not diverging; no intercalated sectors except the postnodal. 11.
11. { Cu₂ reduced to a cross-vein. Subfamily *Protoneurinae*.
Cu₂ normal. 12.
12. { Quadrilateral regular. Subfamily *Platycneminae*.
Quadrilateral irregular, usually with distal angle sharply acute. Subfamily *Agrioninae*.

EXPLANATION OF PLATES XXXII.-XXXIV.

Plate xxxii. (Photomicrographs).

Diphlebia lestoides Selys.Fig. 1.—Penultimate larval instar. Middle portion of wing; ($\times 60$).Fig. 2.—Penultimate larval instar. Basal portion of wing; ($\times 60$).Fig. 3.—Antepenultimate larval instar. Whole wing; ($\times 25$).

Plate xxxiii. (Photomicrographs).

Diphlebia lestoïdes Selys.

Fig.1.—Penultimate larval instar. Basal two-thirds of wing; ($\times 25$).

Fig.2.—Last larval instar. Cuticularisation. Middle portion of wing; ($\times 60$).

Fig.3.—Last larval instar. Cuticularisation. Basal portion of wing; ($\times 60$).

Plate xxxiv. (Photomicrographs by Dr. F. Ris).

Calopteryx splendens Harris.

Fig.1.—Last larval instar; ($\times 25$).

Fig.2.—Last larval instar. Base of wing; ($\times 60$).

Fig.3.—Penultimate larval instar. Basal half of wing; ($\times 60$).



Tillyard, R. J. 1915. "On the development of the wing-venation in zygopterous dragonflies, with special reference to the Calopterygidae." *Proceedings of the Linnean Society of New South Wales* 40, 212–230.

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