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FURTHER RESEARCHES UPON THE PROBLEMS OF  
THE RADIAL AND ZYGOPTERID SECTORS IN  
THE WINGS OF ODONATA, AND UPON THE  
FORMATION OF BRIDGES.

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(Six Text-figures.)

My previous studies upon the problem of Dragonfly wing-venation (2, 3) have conclusively shown that the sub-Order Zygoptera differs from the Anisoptera in possessing no sector to the radial trachea. The latter is straight and unbranched in the Zygoptera. The place occupied by Rs in the Anisoptera, viz., between  $M_2$  and  $M_3$ , is filled in the Zygoptera by an additional trachea branching off from M. This I have termed the Zygopterid sector, Ms. As the imaginal wing-venation has to be interpreted by means of the precedent tracheation of the larval wing-sheath, I have logically applied the same terms to the venation.

Now, in a former paper (2), I indicated one genus, *Neosticta*, which might possibly prove an exception to the above rule. In the wings taken from a larva of this genus, I thought that I could distinguish a true trachea Rs. The pigmentation of the wing-sheath, however, was so dense, and the specimen so far advanced towards metamorphosis, that the decision had to be held in suspense, pending the discovery of more material. Since that time, I have carefully examined a large number of larval wings of genera belonging to all three Zygopterid families (*Calopterygidae*, *Lestidae*, and *Agrionidae*) without discovering a single exception to the rule stated above, viz., that R is unbranched in Zygoptera. Thus it became more than ever im-

portant that the doubt concerning *Neosticta* should be cleared up.

Unfortunately, *Neosticta* is a rare genus, the larvæ being only obtainable from one locality, Heathcote, twenty-one miles south of Sydney. These larvæ are rock-dwellers, somewhat resembling those of *Diphlebia*, but much smaller, and possessing two-jointed caudal gills. They live in the deep pools of clear cold water in Heathcote Creek and the Woronora River, and are only to be got by hauling rocks out of these recesses.

Thanks to the kindness and energy of Mr. F. W. Carpenter, M.A., Science Master at Sydney Grammar School, I was enabled to obtain, in August last, five well-grown larvæ of *Neosticta canescens* from Heathcote. Four of these were in excellent condition for study, having only recently entered the last larval instar. The fifth was more advanced, being, in point of fact, at almost exactly the same stage as the one previously examined.

A preliminary examination of one of the cut-off wings of this last larva showed that it closely resembled the one studied and figured in my previous paper (2, Pl. xiii., fig.4). The pigmentation was very dense, and there was the same appearance of Rs descending from R as before. However, when this condition was studied under strong transmitted light, it was at once seen to be due to the cuticularisation of the wing-sheath, already noticed by me in the case of *Diphlebia* (3, p.227). There was no sign of the presence of a trachea Rs at all.

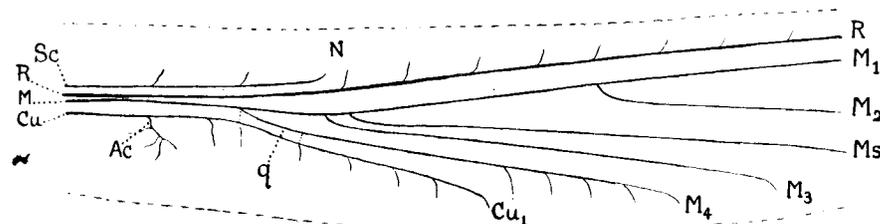
Turning then to the less advanced larvæ, it was an agreeable surprise to find that the dissected-off wings were moderately transparent, so that the tracheation could be easily followed out in detail. All four wings of each of the four larvæ were carefully studied. Of the sixteen, fourteen agreed exactly with the results obtained for all other *Agrionidæ*, viz., R is simple and unbranched, and Ms arises from the main stem of M between  $M_2$  and  $M_3$ . The other two wings (one being a right forewing, the other a right hindwing) showed a peculiar aberration, the origin of  $M_3$  having become shifted on to Ms near its base. This peculiarity at once struck me as being of the utmost importance as evidence of the true nature of bridges and oblique veins, and

will be dealt with fully later on in this paper. The normal tracheation is shown in Text-fig.1, the aberration in Text-fig.4.

Having thus satisfied ourselves that *Neosticta* is in line with all other Zygoptera in possessing an unbranched radius and a Zygopterid sector, Ms, arising from M or one of its branches, let us now review the whole question at issue. This is a very fundamental one, and may be put as follows:—

*Is the Zygopterid sector, Ms, homologous with the Radial Sector, Rs, of Anisoptera, or merely analogous with it?*

In a previous paper (3), I contended that the two were not homologous. No rebuttal of the evidence there adduced has appeared in print; but I have received numerous criticisms,



Text-fig. 1.

Normal tracheation of larval wing of *Neosticta canescens* Tillyard.

ranging from a complete acceptance of my views (Dr. F. Ris), down to an absolute unwillingness to agree with them, in spite of the evidence I have selected Dr. P. P. Calvert's criticism as a very fair statement of the case in favour of the homology between Rs and Ms. He writes as follows:—

“If  $M_1$ ,  $M_2$ ,  $M_3$ , and  $M_4$  are homologous in Zygoptera and Anisoptera, as you say on p.224 (3), is there not something *more than the analogy* between the Anisopteran Rs and the Zygopteran Ms which you recognise on the same page? If Zygoptera and Anisoptera had a common origin, must not Ms and Rs have come from one and the same primitive trachea? If this be the case, then the distinction between Ms and Rs is really not such a fundamental one after all. If, on the other hand, Anisoptera and Zygoptera had not a common ancestry, then the apparent

homologies of the other tracheæ are only the result of convergence (a position I can't admit), and Rs and Ms are really quite different things. I should be glad to have your explanation of these difficulties (as they seem to me)."

Now this is a very lucid statement of the case, and one with which I must confess great sympathy. Like Dr. Calvert, I could not for a moment admit that Anisoptera and Zygoptera had no common ancestry, though I would hold, perhaps, that the cleavage between them is greater, and that the common ancestry lies further back in geological time, than Dr. Calvert may be prepared to grant. For this reason, I felt that the researches which I had carried out could not be left in their present state. Having satisfied myself that *Neosticta* (the only doubtful genus) falls into line with all the rest, I was spurred on, by Dr. Calvert's very reasonable statement of the case, to investigate the whole problem as fully as possible, so as to review the whole evidence, and to come to some definite conclusion.

In order to delimit the problem, let me state clearly at the start that, as far as I can see it, we have actually two cognate problems to deal with. The first of these concerns the relationship between *trachea* Rs and *trachea* Ms, the second that between *vein* Rs and *vein* Ms. As we shall see in the sequel, these two problems may very well lead to different results.

Leaving aside altogether the question of palæontological evidence, which cannot be admitted into this problem satisfactorily, owing to the complete absence of the tracheational interpretation of fossil vein-formations, I have classed the available evidence under three main headings:—

(1) *The structural evidence.* By this I mean the evidence obtained from a study of the wing-tracheation of the last larval instar, and the interpretation of the corresponding imaginal wing-venation.

(2) *The ontogenetic evidence.* This is the evidence obtained from the tracheation of the wings of the developing larva, from the earliest examinable stage up to the last instar.

(3) *The evidence from Bridges and Oblique Veins.* The connection of these structures with the problem in hand is not, per-

haps, at first evident. Actually, they assume a position of immense importance, and must be fully dealt with if the problem is to be solved.

I propose now to take these three kinds of evidence in full, and to draw definite conclusions from them.

1. *The Structural Evidence.* (Text-figs. 1, 3).

We may best marshal this by gathering together all the results of wing-tracheational studies by different students of the Order, and arranging them in tabular form. I have before me the published results of Professor Needham (1) and myself (2, 3), together with the beautiful series of photographs taken by Dr. Ris from the larvæ of *Libellula*, *Calopteryx* (3, Plate xxxiv.), and *Ischnura*. No doubt other students have examined other genera; but, as their statements have not been published, they cannot be here included.

The point to notice is that the evidence is, *without a single exception*, in favour of the view that *trachea* Rs in Anisoptera is *not homologous with trachea* Ms in Zygoptera. It follows also that, if the veins Rs and Ms in the imaginal wing are laid down in their entirety upon the previously existing tracheæ Rs and Ms respectively, then *vein* Rs in Anisoptera is *not homologous with vein* Ms in Zygoptera. This second conclusion must not, however, be accepted without a fuller examination of the interplay of tracheational and venational developmental forces, which are discussed later on, on p. 879.

The following table exhibits the results obtained :—

TABLE OF GENERA EXAMINED FOR WING-TRACHEATION.

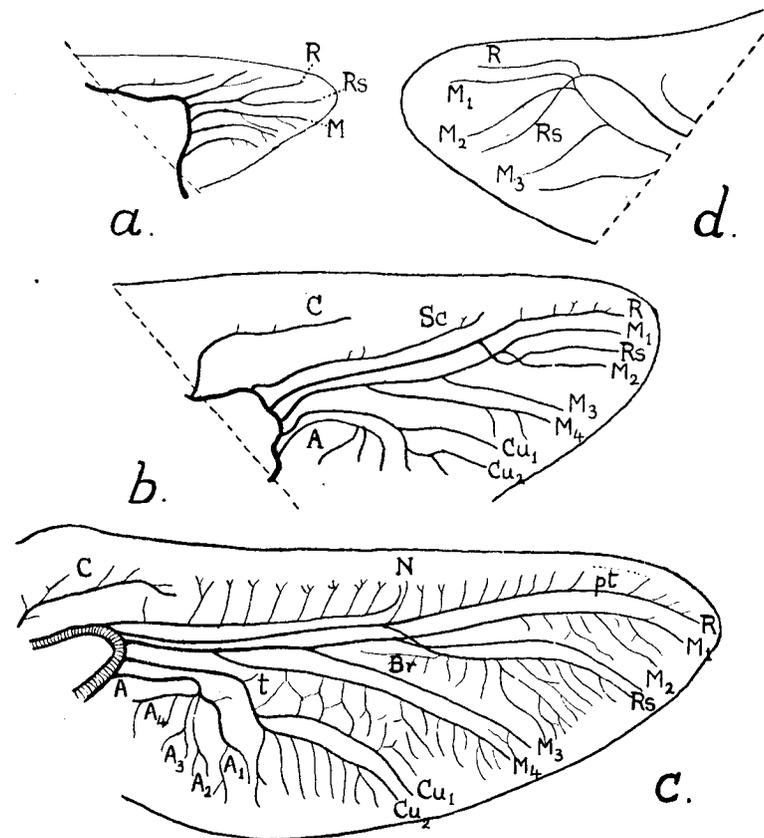
(N=Needham, R=Ris, T=Tillyard.)

ZYGOPTERA.	ANISOPTERA.
R simple and unbranched. An extra trachea, the Zygopterid Sector Ms, developed from M between M <sub>2</sub> and M <sub>3</sub> .	R once branched, the branch being the Radial Sector Rs, which crosses M <sub>1</sub> and M <sub>2</sub> , so as to come to lie between M <sub>2</sub> and M <sub>3</sub> .
Families CALOPTERYGIDÆ and AGRIONIDÆ. Ms arises from the main stem of M.	Family ÆSCHNIDÆ. * <i>Gomphus</i> (N) <i>Lanthus</i> (N) <i>Austrogomphus</i> (T) <i>Hemigomphus</i> (T) <i>Cordulegaster</i> (N) <i>Dendroaeschna</i> (T) * <i>Æschna</i> (T) <i>Anax</i> (N and T)
* <i>Diphlebia</i> (T) * <i>Calopteryx</i> (R) <i>Neosticta</i> (T) <i>Isosticta</i> (T) * <i>Argiolestes</i> (T) * <i>Ischnura</i> (R and T) * <i>Calagrion</i> (T) <i>Austroagrion</i> (T)	Family LIBELLULIDÆ. * <i>Synthemis</i> (T) <i>Didymops</i> (N) <i>Austrocordulia</i> (T) <i>Cordulephya</i> (T) * <i>Hemicordulia</i> (T) * <i>Libellula</i> (N and R) <i>Orthetrum</i> (T) <i>Diplacodes</i> (T)
Family LESTIDÆ. Ms arises from M <sub>2</sub> near its base. * <i>Synlestes</i> (T) <i>Lestes</i> (N) * <i>Austrolestes</i> (T)	Total genera examined : 16.
Total genera examined : 11.	

## 2. The Ontogenetic Evidence. (Text-fig.2).

In the table given above, the genera marked \* are those in which more than one larval instar has been examined. In the Zygoptera, it has not been possible to examine more than the four last larval instars (which I have done in *Austrolestes*), owing to the delicacy of the tracheæ. In the earliest examinable stage, R is simple and unbranched in Zygoptera, and remains so up to the last larval instar. Very different is the case with the Anisoptera, in which Needham (1, Fig.1) has shown that, at the

earliest examinable stage, R is strongly and definitely branched (Text-fig.2,a). At a later stage (the exact instar is not noted,



Text-fig.2.—Ontogenetic stages in the development of the larval wing-tracheation in Odonata. a, *Gomphus*, very early stage, 1 mm. wing; b, *Gomphus*, later stage, 3 mm. wing, Rs between M<sub>1</sub> and M<sub>2</sub>; c, *Gomphus*, last larval stage, Rs across M<sub>1</sub> and M<sub>2</sub>, and bridge (Br) indicated; d, *Libellula*, very early stage, 0·8 mm. wing, Rs already across M<sub>1</sub> and M<sub>2</sub>. a-c, after Needham; d, drawn from a photomicrograph taken by Dr. F. Ris.

but it would appear to be the last but three), Needham shows Rs thrown over M<sub>1-2</sub> just before it divides into M<sub>1</sub> and M<sub>2</sub>, and then

crossing  $M_2$  again so as to lie between  $M_1$  and  $M_2$  (Text-fig. 2, b). At the latest stage (Text-fig. 2, c),  $R_s$  is thrown across both  $M_1$  and  $M_2$ , so as to lie between  $M_2$  and  $M_3$ .

Dr. Ris has photographed (Text-fig. 2, d) the triangular wing-bud in a very early stage of *Libellula* (this would appear to be one instar earlier than Needham's earliest stage, since the wing is only 0.8 mm. long, and definitely more triangular in shape than Needham's wing of *Gomphus*, which was 1 mm. long). This shows  $R_s$  already crossing both  $M_1$  and  $M_2$ ! I find the same result in the earliest stages of *Hemicordulia*. But we must remember that the *Libellulidæ* are far more specialised than *Gomphus*. The latter (if Needham's observations are correct, and I see no reason to doubt them) has preserved the ontogenetic stages in detail; the former reaches the final condition of  $R_s$  while the wing is yet very small.

We see, then, that the ontogenetic evidence supports the structural evidence, but with greater force. *How can a trachea which, in the earliest examinable larval stage of Anisoptera, is a branch of R not even crossing M at all, and which only reaches its final position (in Gomphus) by two successive changes, be homologous with the branch of M which is present in a fixed position (between  $M_2$  and  $M_3$ ) in Zygoptera from the earliest examinable stage?* One must either accept the proof as definitely against the homology, or deny one's belief altogether in the Biogenetic Law.

We must conclude then, both on the structural and on the ontogenetic evidence, that *trachea  $R_s$  of Anisoptera is not homologous with trachea  $M_s$  of Zygoptera.*

### 3. The Evidence from Bridges and Oblique Veins.

We have now to approach very cautiously the crux of the whole problem, viz., whether we have been correct in maintaining that the imaginal veins  $M_s$  and  $R_s$  are wholly laid down upon the preceding tracheæ  $M_s$  and  $R_s$  respectively, or whether they may not have, in special cases, a more composite origin.

Thus we have to deal with a question that is even more fundamental than the point immediately at issue, viz., the interaction of the two great forces whose interplay has moulded the Odonate wing from the very start. These are, the force of *tracheational*

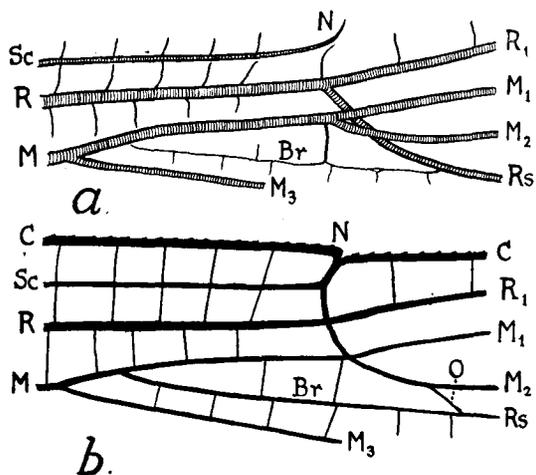
*development*, which is mainly concerned, throughout larval life, with supplying each cell of the developing wing with sufficient oxygen, and the force of *venational development*, which is concerned only with the final production, at metamorphosis, of an imaginal wing-plan best suited to withstand the strains and stresses of flight. Both these forces, in the evolutionary scheme, aim at perfection. But, as they are at any rate to some extent antagonistic the final result must be a compromise. This compromise is best seen, in the imaginal venation, in the formation of *bridges and oblique veins*—structures which, we may well believe, are not wanted at all to ensure perfection of flight, but which have been forced upon the imaginal pattern owing to the trend of tracheational development. On the one hand, the tracheational scheme appears early in the developing larval wing; one might almost imagine that the forces controlling it must have had everything their own way, and that the imaginal pattern, when first laid down in the wing of the last larval instar, must be absolutely dependent upon it. On the other hand, in spite of the long start gained by the tracheational forces, can we doubt that it is the imaginal wing-plan which must be aimed at all along? For, if this be not attained successfully, the type would be weak in flight, and would soon die out.

It is just here that we have to study intensely the problem of bridges and oblique veins. Professor Needham's now famous discovery and explanation of the bridge-veins in Odonata is well-known, but needs to be shortly summarised. In the Anisoptera, the bridge is, according to him, a "brace evolved out of the boundaries of ordinary cells," in order to "correct the mechanical weakness of the unilateral fork" (1, p. 755), (*i.e.*, the fork represented in the imaginal venation by the point of departure of  $R_s$  from  $M_2$  at O). Text-fig. 3 will explain Needham's view of the formation of the bridge.

In Needham's view, also, the bridge is a "trunk *secondarily developed* to connect the radial sector with vein  $M_{1-2}$ ." (1, p. 711).

I think that all students of Odonata, including myself, have, up to the present time, accepted these statements without ques-

tion. My views, however, have now undergone a change, owing to the fact that I have recently seen a bridge formed in the Odonata, as it were under my very eyes, and the process does not agree with Needham's dictum. I refer to the aberrant condition which I discovered in *Neosticta*, and which is figured in



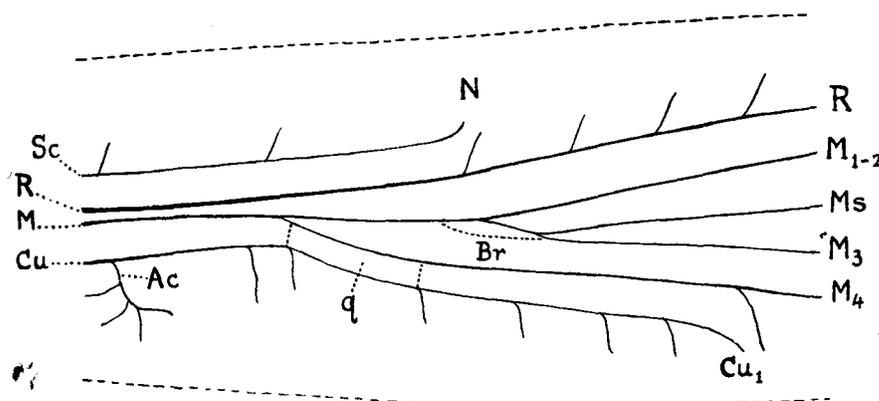
Text-fig. 3.—Formation of bridge (*Br*) and oblique vein (*O*) in Anisoptera (*Libellulidae*). *a*, Tracheation of wing at last larval instar. *b*, Corresponding imaginal venation.

Text-fig. 4. Here is the case of a genus in which, apart from its extreme reduction, the venational plan is simple and primitive. Ordinarily, no bridge is present. Owing to the extreme narrowness of the wing, *M*<sub>3</sub> lies for most of its length very close under *M*<sub>2</sub>. In the aberration, *M*<sub>3</sub> becomes hitched on to *M*<sub>2</sub>, not gradually, by progression distad along *M* towards *M*<sub>2</sub>, but *per saltum*. And the imaginal wing-venation keeps its original position, in the form of the bridge (*br*), clearly visible as a pigment band.

Searching through a long series of imagines of *Neosticta*, I am able to find two wings which have clearly been derived from this aberrant tracheal condition. In both, the change in the position of *M*<sub>3</sub> basally is betrayed by the shortening and slight

obliquity of the cross-vein usually in this position. The cross-vein has, in fact, become an *oblique vein*, and the proximal part of *M*<sub>3</sub> has become a *bridge*.\*

Now, with this example of how a bridge may be formed fortuitously before us, we must ask ourselves whether Needham was right in determining the bridge-vein as a secondary formation.



Text-fig. 4.—Aberrant tracheation of larval wing of *Neosticta canescens* Tillyard. *M*<sub>3</sub> has been captured *per saltum* by *M*<sub>2</sub>. Original course of basal part of *M*<sub>3</sub> persists in the imaginal venation as a bridge (*Br*).

Is it not more rational, after all, to see in the bridge-vein the original basal part of a main vein, while the oblique vein is the sign that the tracheation has become specialised. Let us examine the two well-known cases of Bridge-formation in Odonata in this new light:—

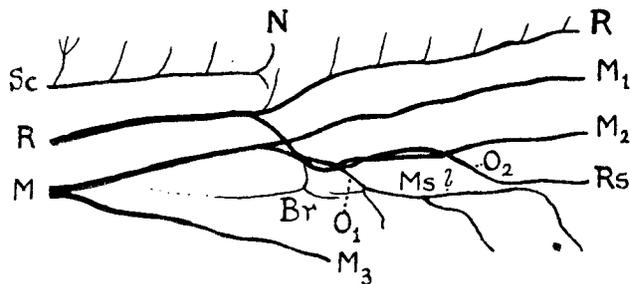
(a) *The long bridge of Lestidae*. If this new view be correct, the *Lestidae* must be derived from ancestors in which *M*<sub>2</sub>, *M*<sub>3</sub>, and *M*<sub>4</sub> all came off separately from *M*. Owing, however, to progressive narrowing of the wing, *M*<sub>3</sub> must have come to lie close under *M*<sub>2</sub> at a point near its base. Finally, trachea *M*<sub>2</sub>

\* It should be carefully noted that this aberration has nothing to do with the long bridge of *Lestidae*, which is caused by *M*<sub>3</sub> becoming attached to *M*<sub>2</sub>.

must have captured trachea Ms *per saltum* just in the same way that trachea Ms has captured trachea M<sub>3</sub> in the *Neosticta* aberration, leaving the original basal portion of vein Ms existing as the long bridge, while the new base of Ms became the oblique vein.

The fact that, in *Synlestes*, the oblique vein cannot always be determined, is evidence in favour of this view. If a large number of larvæ were to be examined, may not some of them still possess the original tracheation in one or more wings? The imaginal venation from such a wing would lack the oblique vein.

It becomes necessary, also, on this new view, to examine the earliest wing-buds of the *Lestidae*, with a view to determining the original position of trachea Ms with respect to M, as shown by the ontogenetic evidence. Such an examination I hope to carry out later on.



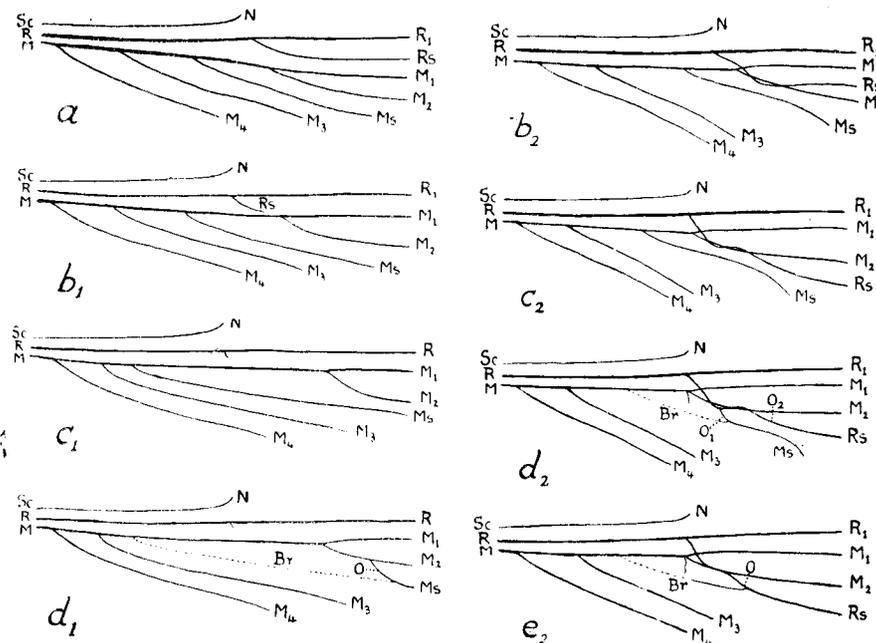
Text-fig. 5.—Formation of the two oblique veins ( $O_1$ ,  $O_2$ ) in *Cordulegaster*.

Ms?, the trachea which, it is suggested, was originally Ms, and has been captured *per saltum* by Rs. Adapted from Needham.

(b) *The bridge of Anisoptera*. In this case, any question of Rs having become hitched to M<sub>2</sub> *per saltum* cannot be entertained, owing to the fact that the ontogenetic evidence is absolutely against it. We must either accept Needham's view of this bridge as correct—*i.e.*, it is secondarily formed to strengthen the unilateral fork—or we must seek for some other explanation.

It is well known that, in the subfamilies *Cordulegastrinae* and *Petalurinae* (the two most archaic subfamilies of the Anisoptera), there are two oblique veins present (Text-fig. 5,  $O_1$ ,  $O_2$ ). This is

due to the fact that trachea Rs in these forms is itself branched. Now, unfortunately, we do not know the ontogeny of the larval wing in these subfamilies. The suggestion I would make is that, in these archaic forms, we have trachea Rs and trachea



Text-fig. 6.—Suggested phylogeny of the Odonate wing in the region of radius, media, and branches. *a*, archaic ancestor of Zygoptera and Anisoptera; *b*<sub>1</sub>-*d*<sub>1</sub>, phylogeny of Zygoptera; *b*<sub>1</sub>, reduction of Rs; *c*<sub>1</sub>, loss of Rs = *Megapodagrionine* stage; *d*<sub>1</sub>, capture of Ms *per saltum* by M<sub>2</sub> = *Lestid* stage (original course of vein Ms preserved as the bridge *Br* in the imaginal venation); *b*<sub>2</sub>-*e*<sub>2</sub>, phylogeny of Anisoptera; *b*<sub>2</sub>, Rs crosses M<sub>1</sub> (*cf.* Text-fig. 2*b*); *c*<sub>2</sub>, Rs crosses M<sub>1</sub> and M<sub>2</sub>; *d*<sub>2</sub>, Rs captures Ms *per saltum* (*cf.* Text-fig. 5); *e*<sub>2</sub>, Ms suppressed (the original course of vein Ms preserved as the bridge *Br* in imaginal venation).

Ms both present, and that, in the last larval instar, the latter trachea becomes hitched on to Rs, just as M<sub>3</sub> became hitched on to Ms in the *Neosticta* aberration. In that case, the whole

bridge, from its origin basally on M up to the second oblique vein  $O_2$ , represents, in the venation, the original Zygopterid sector Ms, with the oblique vein  $O_1$  standing upon it to mark the point where trachea Ms has been captured by trachea Rs. The vein continuing the bridge is the true Rs, of which also  $O_2$  must be an essential part.

The above explanation, as it seems to me, offers the only solution possible in favour of a *partial* homology between veins Ms and Rs, as now present in the wings of Odonata. Text-fig.6 would show, on this supposition, the two lines of development leading to Zygoptera and Anisoptera respectively. For the common ancestor, we should have to postulate a form possessing both a true Rs and a true Ms (Text-fig.6,a). From this, the Zygoptera would be derived by reduction, Rs being entirely eliminated.\* The Anisoptera, on the other hand, would be derived from the ancestral form via the *Petalura-Cordulegaster* stage, trachea Ms being first of all captured by Rs, as in these forms, and then entirely eliminated; while, in the imagines, the short Anisopterid bridge would remain as the *true vein Ms*, and therefore *homologous with* the long bridge of *Lestidae*, and also with the basal part of Ms in the *Calopterygidae* and *Agrionidae*.

This might be exhibited as follows:—

Trachea or Vein.	ZYGOPTERA.		ANISOPTERA.	
	<i>Calopterygidae</i> + <i>Agrionidae</i> .	<i>Lestidae</i> .	<i>Petalurinae</i> + <i>Cordulegastrinae</i> .	Other subfamilies.
Trachea Ms	present, attached to M	present, captured by $M_2$	present, captured by Rs	absent
Trachea Rs	absent	absent	present	present
Vein Ms ...	present in full	present in full (basal portion = long bridge)	present (= bridge)	present (= bridge)
Vein Rs ...	absent*	absent*	present, from $O_2$ to wing-margin	present, from $O$ to wing-margin

The new view of Bridge-formation, embodied in the above

\* Unless, indeed, the subnodal vein itself be the remains of Rs.

discussion and table, may be briefly contrasted with the older (Needham's) view as follows:—

(1) *Needham's view*:—When the fusion or crossing of two main tracheæ causes the formation of a unilateral fork, preceded by a weak area not possessing a main trachea, this weak area and the fork are secondarily strengthened, in the imaginal venation only, by the backward development of a strong vein called a bridge. The base of the unilateral fork persists as the oblique vein.

(2) *The new view*:—When the fusion or crossing of two main tracheæ causes the formation of a unilateral fork, preceded by a weak area not possessing a main trachea, the imaginal venation does not follow this specialisation in the tracheal system, but adheres to the older and more advantageous venational plan. Thus, the imaginal vein originally present *persists as a bridge* along that part of the wing now devoid of a main trachea. The point of attachment of the shifted trachea is represented in the venation by the oblique vein.

The principal argument in favour of the new view seems to me to be this:—If we take any specialised Odonate wing, in which an oblique vein is present, and replace the oblique vein by an ordinary cross-vein, then the venation will be seen to resemble what is admitted to be the most archaic venational plan for the sub-order. For instance, if we cut out the oblique vein from *Lestes* or *Synlestes*, the arrangement of R, M and branches at once becomes similar to that of the archaic *Megapodagrioninae*, in which no oblique vein or bridge has ever been developed. We may well ask, how is it that there is a bridge developed in this position in every form where tracheational specialisation has set in? If Needham's view be correct, then there must have been a period in the evolution of the wing-venation (before the bridge became fully formed) in which the place of the bridge was taken by the irregular boundaries of polygonal cells from which the bridge is supposed to have arisen. Can anyone maintain that such a weakened imaginal form would have been able to hold its own during the evolution of the bridge? Or, if it is argued that the bridge was formed link by

link, as the trachea moved distad, then the answer is that, in *Neosticta*, we see a bridge formed *per saltum*, and there is no evidence that the trachea did move distad gradually. The effort required to construct evolutionally such an immensely long bridge as that of the *Lestidae* in this fashion is almost inconceivable. Moreover, as a support to the unilateral fork at O, it is absurdly misplaced. One would have expected it to run back to M about half-way between Ms and M<sub>3</sub>, if such were the object of its development.

Further, it should be noted that, in other Orders, the formation of an oblique vein through tracheational specialisation does not involve the formation of a bridge. Thus, in the forewing of the *Myrmeleontidae* (4), the vein M<sub>2</sub> comes off from M<sub>1</sub> by means of an oblique vein, but it is continued basad by Cu<sub>1</sub>, and not by a bridge-vein. In the Odonata, if the bridge-vein be Ms, and not a new development, the position is an analogous one.

Here I must leave this fascinating line of inquiry, for which much more evidence would need to be brought forward before it could be regarded as fully established. As regards the main argument, concerning the supposed homology between Ms and Rs, the position may be summed up as follows:—

1. Trachea Ms is *not* the homologue of trachea Rs. On this both the structural and ontogenetic evidence are overwhelming.

2. If we interpret the main veins solely from their underlying main tracheæ, it follows that vein Ms is *not* the homologue of vein Rs.

3. If, however, we allow that the venation may retain the archaic plan, while the corresponding tracheation becomes specialised, then we must alter our view of the significance of bridges and oblique veins. In that case, the long bridge of *Lestidae* may reasonably be regarded as the original vein Ms. In the case of the Anisoptera, the bridge may also represent Ms, while the vein continuing it beyond O is undoubtedly Rs. Thus, the *basal portions* of the veins now called Ms and Rs respectively would be true homologues; the distal portions (beyond the oblique vein, when it is present) are never homologous.

Thus we see that, *under no circumstances can we prove veins Ms and Rs to be complete homologues*. And, until further evidence can be brought forward in support of statement No.3 above, it would seem advisable to retain the notations Ms for Zygoptera and Rs for Anisoptera in their entirety.

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