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The Tracheation of the Wings of Early Larval Instars of Odonata Anisoptera, with Special Reference to the Development of the Radius.

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(Plates X, XI.)

Comstock and Needham in 1898, and Needham in 1903 published an account of the development of the wing venation of the Odonata. In the account of Needham, 1903, the development of the wing veins is traced through a series of larval stages in order to show that the vein lying posterior to *M2*, the subnodal sector of earlier authors, is really the vein *Rs*, and that it has come to lie in this unusual position as the result of a series of evolutionary changes in the history of the dragon fly wing. These evolutionary changes, according to Needham, are indicated in the ontogeny of the larval tracheae. Figs. 1 and 2 in Needham's paper represent drawings of three stages

in the development of the larval wing. These drawings are to show: in fig. 1, A, the primitive condition in which the trachea *Rs* occupies its normal position anterior to *M*1, in fig. 1, B, the second stage, in which *Rs* has come to lie posterior to *M*1 but is still anterior to *M*2, and finally, in fig. 2, the condition obtaining in the full grown larva, in which *Rs* lies posterior to *M*2. The occurrence of these stages in the larval wings constitutes a part of Needham's evidence that the vein lying between *M*2 and *M*3 is the radial sector and is not a true branch of the media.

The work of Tillyard (1922) has again thrown doubt upon the identity of the vein *Rs*, for this author does not concur in Needham's interpretation but states that the *Rs* of Needham is really a branch of the media, although receiving its tracheal supply in part through a branch of *R;* and that the original *Rs* has been cut off by, and become attached to, the media. While admitting that if the ontogenetic stages described by Needham actually occur in the developing wing rudiments of the larva, this would constitute strong evidence in favor of Needham's view, Tillyard doubts that such stages can be demonstrated.

It was suggested to me by Dr. Philip P. Calvert, that in view of the doubts which had thus been cast upon the existence of the two earlier stages described by Needham, it would be desirable to go over the work of that author and examine the tracheation of the earliest larval instars, since an accurate knowledge concerning the condition of the trachea *Rs* at its first appearance and of how it comes to occupy the position it is said to assume in later instars might be of value in solving the difficult problem of the homology of the imaginal vein *Rs*.

The larvae examined were those of *Anax junius* Drury, *Gomphus villosipes* Selys and *Gomphus exilis* Selys. The wing rudiments of these larvae were prepared and mounted essentially after the manner described by Needham. In the case of the younger ones it was necessary, because of the small size of their wings, to cut out the thoracic terga and the first segment of the abdomen in one piece and, without removing or disturbing any of the underlying tissue, to mount the piece thus removed entire. Treated in this way, the wing rudiments

and the delicate tracheae contained in them are subjected to no strain or pressure of any kind and there is practically no danger of the tracheae being displaced from their normal courses. The figures are all from drawings made with the aid of a camera lucida, for it was found that the earlier stages, such as those in which the wings were less than 0.5 mm. in length, could not be photographed, since the high magnifications necessary make it impossible to get all the tracheae in focus together. In the wing measurements given, the term "length" is used to indicate the distance between the mid-point on the line of articulation of the wing with the thoracic tergum and the extreme tip of the wing.

In *Anax*, the smallest larvae possessing wing rudiments which I was able to obtain were 9 to 10 mm. in length. The wings of these larvae were 0.2 to 0.22 mm. long; three such wings, from different larvae, are represented in figs. 1-3. The shortness of these wings compared with their width at base and the less definite arrangement of their tracheae make it immediately apparent that we have to do with a much earlier stage in the development of the wing than in the case of the earliest stages represented by Needham's figures or by Tillyard in his text fig. 3.

In comparing the wings in figs. 1-3, it is noted that there is considerable variation, that there is not a single trachea which is exactly alike in all three figures but that each may vary in the number of its branches and that their arrangement gives but little hint as to the manner of their disposition in the adult. We also note that additional tracheae may often appear between the costa and the subcosta; in fig. 2 there are two such tracheae, in fig. 1 there is one. I am confident in assuming that in all cases the extra tracheae are between *C* and *Sc* and that *M* is always adjacent to *R*, for I have never found, at any stage in *Anax*, any indications of extra tracheae inserted between *R* and *M*. Thus I have found, as Needham did, that in the earliest stage in the development of the wing there are six principal tracheae. The additional tracheae of which there may be one or more inserted between *C* and *Sc*, may persist through later instars but always remain small and are of no importance.

It is noted too, that variability in the number of branches also characterizes the radius and media in this primary stage. In figs. 2 and 3, *R* is two-branched, while in fig. 1 it is unbranched. The media is five-branched in fig. 2, while in figs. 1 and 3 it is in its more usual four-branched condition. Finally it may be noted that the posterior two tracheae are three-branched in fig. 2, and that in figs. 1 and 3 they are two-branched. In regard to the costa it might be mentioned that, at least in *Anax*, this trachea almost always arises not from the same tracheal trunk as do the other wing tracheae, but from a branch of this trunk, the accessory costo-radial trunk, which passes out of the base of the wing. This condition is seen in figs. 2-8; in fig. 1 the costa arises from the same trunk as do the other tracheae. In *Gomphus*, the costa arises either directly from the transverse basal as do the other wing veins, or from the accessory costo-radial trunk as it does in *Anax*.

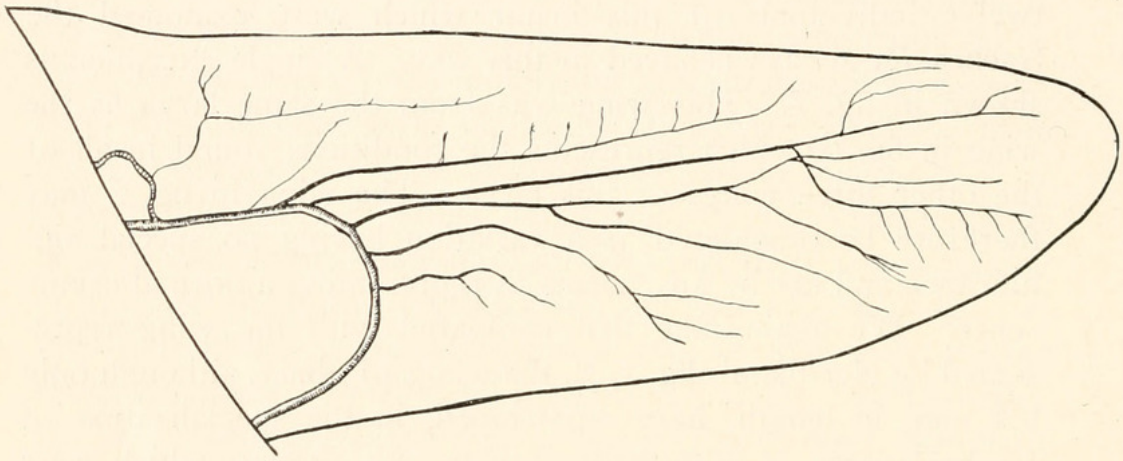
Returning to the radius and observing the course of its branches in the earliest stages, we note that there is no crossing of any branch of this trachea over any part of the media. In fig. 1 the radius is not branched at all and is entirely remote from the media. In figs. 2 and 3 the radius has two branches, the posterior branch being, according to the view of Needham, the radial sector. This posterior branch, which for the present I will continue to refer to as *Rs*, is in this stage entirely free, and remote from the media. This observation apparently agrees with that of Needham, who illustrates such a condition in his fig. 1, A, if we disregard the difference in the sizes of the wings in the two cases. We must, however, remember that the wing rudiments represented in figs. 1-3, are in a much earlier stage of development than that figured by Needham which, he states, was 1 mm. long, as is indicated by their smaller absolute size, the difference in the proportions of length to width and in the great variability in the arrangement and in the number of branches of the various tracheae.

Figs. 4-7 represent the tracheation of the wing rudiments taken from *Anax* larvae whose body length was 13 to 13.5 mm. These larvae are apparently of the instar following upon that of the larvae just discussed, since on frequent collecting trips

during August and September no larvae of an intermediate body length were found, although those of 10 mm. and those of 13 mm. were quite plentiful. The wings of this instar were 0.4 to 0.45 mm. long, the tracheation in them was much less variable than in those of the preceding instar. The additional tracheae, often so prominent in the previous instar, were less frequently observed or were at least comparatively smaller and of little importance. Other tracheal branches, especially those of *R* and *M*, heretofore simple, are in this stage composed of two or more fine branches which tend to cling together. The radius is, in all cases, at least two-branched, a posterior branch *Rs* crosses over the two anterior branches of *M*. In all of the twelve individuals of this instar which were examined the trachea *Rs* always behaved in this way. A single exception is shown in fig. 7. This wing was from the same larva as the wing in fig. 6, which represents the conditions found in all of the other three wings of this larva. The wing in fig. 7 may therefore be considered as a variation having no special significance and not by any means as representing a normal occurrence. We again note that compared with the wing represented by Needham's fig. 1, B, the wings of *Anax*, although only 0.4 mm. in length, have outstripped, in the specialization of tracheal paths as regards *Rs*, wings of *Gomphus* which were (*teste* Needham) 3 mm. in length, whilst in regard to many other features the *Anax* wings are far behind the *Gomphus* wings of Needham. Not only is the wing in Needham's figure much larger and more elongated (its length being greater than its width at base) than the wings in my figures, but the tracheae themselves, with the exception of *Rs*, speak of a more advanced stage of development. All the tracheae, excepting *C*, are comparatively closer together at their origin and along their parallel courses; *Cu* and *A* have taken on quite decidedly the characteristic paths which they assume in anticipation of the formation of the triangle; the nodus and the stigma are already indicated; and finally, the tracheal trunk supplying the wing tracheae describes an arc of a comparatively shorter radius, a condition more typical of later instars.

Fig. 8 represents a wing rudiment of the next succeeding in-

star, the larva being 15 mm. long and the wing 0.65 mm. in length. Here we note again that *Rs* crosses over *M*1 and *M*2. The branches of *R* and *M* are composed in their distal portions of bundles of fine tracheae lying close together and often winding about each other, a condition already noted in the preceding instar and which has now become more pronounced. *C* and *Sc* have also developed a number of fine branches in this instar. This wing too, has many features in addition to its much smaller size, which indicate that it is in an earlier stage of development than that of Needham's fig. 1, B, which shows *Rs* as lying between *M*1 and *M*2.



Text Fig. A.—Wing rudiment from larva of *Anax junius*; length of larva 33 mm., length of wing 1.9 mm.

Finally, in text fig. A, there is represented a wing 1.9 mm. long, taken from a larva 33 mm. long. The wing in this stage is considerably elongated and the fascicled condition of the ends of the branches of *R* and *M* has been abandoned.

(To be continued.)

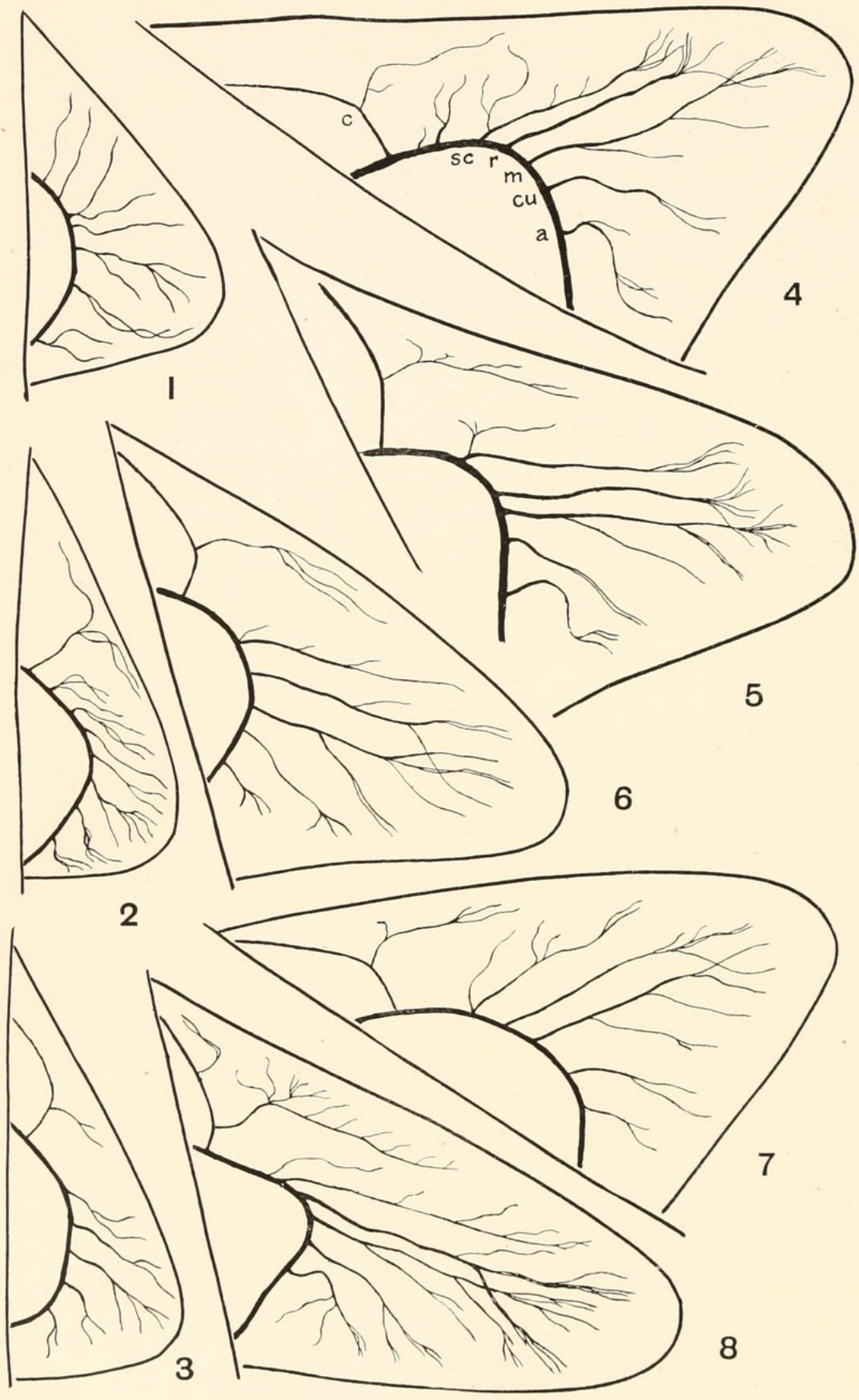
EXPLANATION OF PLATE X.

Figs. 1-8. Wing rudiments from larvae of *Anax junius*.

Figs. 1-3, Length of larvae 9 to 10 mm., length of wings 0.2 to 0.22 mm.

Figs. 4-7, Length of larvae 13 mm., length of wings 0.4 to 0.45 mm.

Fig. 8, Length of larva 15 mm., length of wing 0.65 mm.



TRACHEATION OF WINGS OF EARLY LARVAL INSTARS OF ANAX JUNIUS.—SCHMIEDER.