ON SOME PROBLEMS CONCERNING THE DEVELOPMENT OF THE WING-VENATION OF ODONATA.

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(Plates xi.-xiii., and twenty text-figures.)

INTRODUCTION.

During the course of some researches into the tracheal system of Odonate larvae, I had occasion to examine a very large number of these interesting creatures. Thus a beautiful series of developing nymphal wings was presented to me, which it was impossible to ignore or to cast away unexamined. Hence it was that I determined to photograph the wings of each species, as opportunity offered, and to use them with a view to familiarising myself with the problems and theories set forth by Needham in his now famous paper.*

It soon became evident that there were certain portions of the question in hand that needed special attention, while new aspects of the problem presented themselves to my mind and demanded investigation. It seemed to me that the whole problem of the development of the unique venation of the Odonate wing might conveniently be divided into two parts, viz.:

i. The study of the tracheae of the developing wing, and their relationships to the imaginal wing-veins.

ii. The study of the source of the oxygen-supply of the wing-tracheae.

Now Needham's paper deals with i, only, and that chiefly in so far as it concerns the Anisoptera. The investigations into the Zygoptera seem to have been on a much smaller scale, and it is very evident that a wide field of research remains open in this direction. With regard to the Anisoptera, it seemed to me that the study of the anal tracheae had been left in a somewhat unsatisfactory state. Hence I have devoted a considerable part of my paper to an elucidation of this problem, with special reference to the development of the so-called anal loop.

With regard to ii, it seems quite clear that the wing-venation cannot be fully understood until we go to the root of the problem. That is to say, we must go a stage back beyond i., and enquire carefully how the oxygen-supply is brought to the wing-tracheae; or, in other words, we must connect up these wing-tracheae with the complex tracheal system of the larva, and study the connection between them.

The general tracheal system of the Odonate larva is so peculiar that it might well be suspected of exercising some special influence on the developing wing. Its chief peculiarity is the fact that the oxygen-supply is derived in all cases from the anal end of the body during practically the whole period of growth; either by means of the internal "branchial basket" in the rectum of Anisoptera, or by the external caudal gills of Zygoptera. Hence, chiefly by means of the huge dorsal tracheal trunks, but also in a less degree by the visceral and ventral trunks, the oxygen is conveyed forwards to all parts of the body. As regards the head and thorax, the supply comes entirely from the dorsal trunks, since the ventral trunks do not reach so far forward, and the visceral trunks send only their attenuated anterior ends into the thorax to connect with the tracheae of the middle leg.

Now in all cases so far investigated, the tracheal supply of the developing wings of insects has been found to arise from two sources*:

A. A branch from the great dorsal trunk enters the costal side of the wing-base and supplies the costo-radial group of wing-tracheae (viz., costa, subcosta, radius and media).

B. A branch from the ventral trunk enters the anal side of the wing-base and supplies the cubito-anal group of wing-tracheae (viz., cubitus and analis).

In all cases, except Plecoptera and some Cockroaches, the branches A and B are connected by a transverse trachea, so that a continuous loop is formed passing from the dorsal trunk into the costal side of the wing-base, thus making a loop projecting slightly into the wing-base (from this loop the wing-tracheae arise in order), and finally leaving the wing-base at its anal side and joining the ventral trunk.

It is quite clear, therefore, from the start, that this last connection with the ventral trunk could not exist in Odonate larvae; since this trunk does not enter the thorax. However, it is equally clear that a complete loop exists in the base of the wing-rudiment, since it can be seen both in the living larva, and in the cut-off wing-cases. I propose to call this loop the alar trunk (AT), since it is the trachea from which all the principal longitudinal tracheae of the wing arise. The question of its connections costally and anally with the general tracheal system, will be fully dealt with in Part ii. of this paper.

It is fitting that I should state here how valuable and inspiring I have found Professor Needham's work, already quoted. It is, indeed, a solid and excellent foundation, on which all future researches on Odonate wing-venation must be built, and a work that merits the highest meed of praise. Nor can I pass on without recording my indebtedness to all those who, during my long period of ill-health, have so generally assisted me in obtaining the many rare larval forms necessary for the work in hand. For these, I have to thank my wife, Mr. F. W. Carpenter, M.A., Mr. Gregory Geake, and my brother, Mr. S. J. Tillyard.

Owing to the fact that the wing-cases of so many larvae are very deeply pigmented, and sometimes also very hairy, I have adopted the plan of illustrating this paper by drawings traced

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The following is a complete list of the genera and species studied:

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Genus</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gomphinae</td>
<td>Austrogomphus</td>
<td>A. ochraceus Selys.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A. heteroclitis Selys.</td>
</tr>
<tr>
<td>Eschninae</td>
<td>Austrophlebia</td>
<td>A. costalis Tillyard.</td>
</tr>
<tr>
<td></td>
<td>Austrophlebia</td>
<td>A. multipunctata Martin.</td>
</tr>
<tr>
<td></td>
<td>Austrophlebia</td>
<td>A. longissima Martin.</td>
</tr>
<tr>
<td></td>
<td>Cordulinae</td>
<td>D. conspersa Tillyard.</td>
</tr>
<tr>
<td></td>
<td>Synthemis</td>
<td>E. brevistyla Ramb.</td>
</tr>
<tr>
<td></td>
<td>Anax</td>
<td>A. papuensis Burm.</td>
</tr>
<tr>
<td></td>
<td>Cordulinae</td>
<td>S. macrotigma orientalis Tillyard.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>S. eustalacta Burm.</td>
</tr>
<tr>
<td></td>
<td>Metathemis</td>
<td>M. guttata Selys.</td>
</tr>
<tr>
<td></td>
<td>Austrocordulia</td>
<td>A. refracta Tillyard.</td>
</tr>
<tr>
<td></td>
<td>Hemicordulia</td>
<td>H. tau Selys.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>H. australis Ramb.</td>
</tr>
<tr>
<td></td>
<td>Cordulephyia</td>
<td>O. papuensis Selys.</td>
</tr>
<tr>
<td></td>
<td>Orthetrum</td>
<td>O. eulononemus Br.</td>
</tr>
<tr>
<td></td>
<td>Diplocodes</td>
<td>O. silvistidium Br.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D. bipunctata Br.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D. hematodes Burm.</td>
</tr>
</tbody>
</table>

This list comprises thirteen genera (properly fourteen, since Austrogomphus heteroclitis Selys, is not congeneric with A. ochraceous Selys), and nineteen species. It is fortunate that the Cordulinae are so well represented in Australia, since the principal changes in the anal area of the wing take place in this subfamily.

In his remarks on the anal trachea (A.), Needham (loc. cit., p.721) points out that it fuses with the cubitus(Cu) close to the base, and later on branches away from it. This fusion was seen in all Anisoptera examined by him. It occurs also in all the forms which I have examined; so that we may be fairly certain that it is as universal an occurrence as the fusion of the radius with the media.

The very great importance of this basal fusion of Cu and A, and its bearing on the imaginal wing-venation, seems to have from actual photomicographs taken by myself. In these, it is both permissible and desirable to omit all traces of the permanent wing-venation, except such as immediately concern the question in hand. The resulting incompleteness is more than compensated for by the clearness of view thus gained. I have, however, reproduced, in the Plates, such photomicographs as are most essential to the discussion, in order that their interpretation should not be allowed to rest upon my own drawings.

The contents of the paper may be arranged as follows:

Part i.—The study of the tracheae of the developing wing; and their relationships to the imaginal wing-veins (p.166).

Section A.—The development of the anal trachea in Anisoptera, and its relationships to the cubitus, anal loop, and anal triangle (p.166).

Section B.—The occurrence of a bridge-vein in Zygoptera (p.190).

Section C.—The general tracheation of the larval wing in Zygoptera, and its homologies with that of the Anisoptera (p.194).

Part ii.—The study of the source of the oxygen-supply of the wing-tracheae (p.204).

Section A.—Description of the tracheal system of the thorax (p.204).

Section B.—General theory of the unique development of the Odonate wing-venation (p.207).

Part i.

The study of the tracheae of the developing wing, and their relationships to the imaginal wing-veins.

Section A.—The development of the anal trachea in Anisoptera, and its relations to the cubitus, anal loop, and anal triangle.

For the purpose of this section, I studied all the Anisopterous larvae available within a radius of one hundred miles of Sydney, except some of the rarer species, which I failed to obtain. In all, the wings of nearly fifty larvae, in different stages of development, but chiefly nearly full-grown, were cut off and examined. From these, a set of more than forty photomicographs was prepared, giving a wide view of the problem in hand.
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Two very important facts need to be emphasised in connection with it:—

(1). The so-called “first cubito-anal cross-vein” of Needham is not a true cross-vein at all, but is formed about the anal trachea itself, at the point where it descends from Cu. It may be called the anal crossing (Ac).

(2). The so-called “anal vein” of Needham is not a true anal vein, i.e., not developed along the anal trachea, but is a secondarily formed bridge-vein from the lower end of Ac back towards the wing-base, to which it is connected posteriorly in a manner different from the other main veins. Hence the correct notation for this part of the wing is as follows:

The cubitus (Cu) of the imaginal wing becomes Cu + A as far as Ac.

The “anal vein” (A) must be distinguished as the secondary anal vein, and designated A'.

To make these points quite clear, let us compare the nympha! and imaginal wings of Aechna brevistyla Ramb. (Figs.1-3, and Plate xi., figs.1-2). The course of the anal trachea is best followed in the hindwing.

The convergence of A towards Cu near the base, as also that of M towards R, is primarily due to the gradual narrowing of the base of the developing wing in comparison with its length. At first, all these tracheae are separate; but by the time the wing-cases are half-grown, the fusion of Cu + A, as well as that of R + M, can be clearly seen. As the wing grows, the fusion becomes greater, until, in the nearly full-grown nympha!, A is seen to run obliquely up to join Cu very near its base, and then runs closely alongside it as far as Ac. At this point, A turns sharply downwards away from Cu, in the same manner that M turns away from R at the arculus. Hence Ac is the exact analogue of the upper portion of the arculus. It is, for this reason, that at least one “cubito-anal cross-vein” occurs in every Odonate wing.

At the lower end of Ac, A branches into two, just as M branches into two when leaving the arculus. These branches were primarily an upper one, A 1.3 , and a lower one, A 4 , exactly comparable to M 1.3 and M 4 . But owing to the altered shape of the wing-area to be supplied, the upper branch A 1.3 becomes a distally-running branch, while the lower branch A 4 becomes a basally-running branch. In the half-grown Aechna-wing, the two branches may be seen in this position, A 1.3 running distally from Ac and giving off in turn A 1 , A 2 , and A 3 , while A 4 runs basally back from Ac (Fig.1). Later on, owing to the devel-
of the strong anal triangle in the male, or the corresponding rounded portion of the wing in the female, \( A_1 \) tends to migrate from \( A_1 \) across \( A_C \) to become attached to \( A_1 \) very close to \( A_C \). But, in the forewing, it still remains attached to \( A_1 \).

Let us now study the four branches of \( A \) from the base outwards. Firstly, \( A_1 \) is a short, weak trachea, only reaching back from \( A_C \) to about half-way towards the wing-base. In many forms, it comes downwards at its end. Towards the posterior edge of the true wing-base, the line of \( A_1 \) parallel to \( Cu + A \) is continued by the formation of the secondary anal vein \( A' \), which becomes attached to the wing-base of the imaginal wing. Hence we see that \( A' \) is a bridge-vein continuing the weak trachea \( A_1 \) back to the wing-base; its distal portion is formed about \( A_1 \) itself, but its basal portion is not formed about any important tracheal branch at all. It is comparable, therefore, to the "bridge-vein" connecting \( R_1 \) back to \( M_1 \), which occurs in all Anisoptera.

Secondly, \( A_2 \) is a fairly strong trachea descending (primarily) from \( A_1 \) (Fig.1), or (secondarily) from \( A_C \) or \( A_1 \) (Fig.2), towards the posterior border of the wing. About it, in the imaginal wing, the distal side of the anal triangle is formed in the male (Fig.3). In the female, it is usually less regressed towards the base, and generally descends straight from \( A_C \), though individual variations, both basad and distad, are sometimes seen. It gives rise, in the female imago, to a descending vein of less importance than the distal side of the triangle in the male, but corresponding to it. The fate of this branch, in both sexes of the Libellulinae, is of interest, and will be followed out later.

Thirdly, \( A_3 \) is a strong branch descending sharply from \( A_1 \), somewhat distad from \( A_C \), and roughly parallel to \( A_1 \). In the Eschninae (and, indeed, in all forms in which a "loop" is developed) it forms the proximal or basal side of the "anal loop" (AI, Fig.3).

Fourthly, \( A_4 \) is a strong trachea which continues distally towards \( Cu_n \), which it meets quite close under the point of bifurcation of \( Cu_1 \) from \( Cu_n \). It then fuses with \( Cu_1 \) for some distance, turning slantly downwards to run alongside it, and finally leaves \( Cu_n \) by bending downwards and backwards, so as to complete the formation of the distal side of the "anal loop." In the genus Eschna, it bifurcates, near its end, into two small branches. One of these turns basad to join \( A_n \), thus completing the closure of the anal loop; while the other turns away distad in a curve, and helps to form the well-known secondary loop of this genus (AI', Fig.3). The fate of \( A_n \), in the Libellulinae, is also of great interest, and will be dealt with later on.

Having traced the course and fate of the various branches of \( A \) in Eschna, we may now exhibit, in a table, the complete comparison between the two pairs of combined tracheae, viz., \( R + M \) and \( Cu + A \).

<table>
<thead>
<tr>
<th></th>
<th>( R + M ) combine</th>
<th>( Cu + A ) combine</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2-branched tracheae</td>
<td>4-branched tracheae</td>
</tr>
<tr>
<td>First branch</td>
<td>( R_1 )</td>
<td>( M_1 )</td>
</tr>
<tr>
<td>Second branch</td>
<td>( R_s )</td>
<td>( M_2 )</td>
</tr>
<tr>
<td>Third branch</td>
<td></td>
<td>( M_3 )</td>
</tr>
<tr>
<td>Fourth branch</td>
<td></td>
<td>( M_4 )</td>
</tr>
<tr>
<td>Point of departure</td>
<td>Areolus (arc.)</td>
<td>Anal-crossing (A')</td>
</tr>
<tr>
<td>Backward vein</td>
<td>[Upper side of triangle]</td>
<td>Secondary anal vein (A')</td>
</tr>
<tr>
<td>Supplementary sector under lower branch of two-branched tracheae</td>
<td>( \text{Rep} )</td>
<td>( \text{Cu} ) ( \text{pl. (only in Libellulidae, vide infra)} )</td>
</tr>
</tbody>
</table>

In the above table, corresponding parts in the two main columns are true analogues of one another, except in one case, viz., the upper side of the triangle. This is, of course, not analogous to \( A' \), but it is included in the table in brackets in order to call attention to the manner in which it continues \( M \), backwards, just as \( A' \) continues \( A \), backwards.

We turn now to the study of the Anal Loop. The structure known by this name is found throughout the Eschninae and the whole series of the Libellulidae. But whereas it varies very little in shape throughout the Eschninae, it exhibits very great diversity of form in the Libellulidae. On the one hand, we have
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The wide, roundish loop of *Macromia* and *Synthemis*, while, on the other, we see the extremely elongated and narrow, foot-shaped or Italian* loop of the majority of the *Libellulinae* and the *Eucordulini*.

There are two theories in the field to account for the development of this remarkable Italian loop. They may be termed the Theory of Double Descent, and the Theory of Single Descent respectively. They are of special importance, because the whole of one's view of the phylogeny of the *Libellulinae* depends upon which theory one is willing to accept.

The Theory of Double Descent postulates a separate origin for the *Eschnine* and *Macromian* loops, on the one hand, and the Italian loop on the other. As formulated by Dr. Ris,† and up till now accepted by the majority of students of the *Odonata*,‡ it depends mainly on the following interpretation of the venation of the two forms of loop concerned (Fig. 4a). The *Eschnine* and *Macromian* loops are enclosed (as shown above) by A₁ as basal side, and A₂ as distal side. But the Italian loop is formed with A₁ as basal side, and A₂ as distal side, while A₁ forms its strong midrib. Hence the two forms of loop are not homologous, and cannot be descended along a single line. According to the exponents of this theory, the *Libellulinae* are descended from narrow-winged forms similar to *Tetrathemis*, *Cordulephya*, *Agrigomphus*, and hence the Italian loop arose by secondary broadening from this narrow form of wing.

The Theory of Single Descent, which I formulated in 1912,§ postulates a single line of descent for all the different known forms of anal loop. Without attempting to homologise the corresponding parts of the *Eschnine* and Italian loops, it was a protest against the assumption of a double origin for two essentially similar formations; and, in particular, it was a special protest against the assumption that the narrow-winged forms, such as *Tetrathemis*, *Cordulephya*, *Agrigomphus*, lay anywhere close alongside the main line of descent of the *Anisoptera*. In brief, I considered all such narrow-winged forms to be highly specialised asthenogenetic offshoots from the main stem, while the main line of advance had consisted of broad-winged forms from the very beginning; and hence, there could be only one origin for all kinds of anal loop. The notation that agrees with this theory is given in Fig. 4b.

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* I suggest this as a convenient name for this form of loop, which much resembles the map of Italy in shape.
† See diagram of typical *Libellulinae* wing (*Scapanea frontalis* Burm.) in Dr. Ris' *Libellulinen*, Fasc. i.-xvi. of de Selys' Monographs, 1910-1914.
‡ In the short account of the anal loop given by Needham (loc. cit., p. 722), there is nothing to indicate that he favoured this theory. On the contrary, his words, so far as they go, seem to oppose it, but no lettering is attached to his figures of loops. It seems unlikely that the question of a double descent ever occurred to him. The theory was, however, a direct outcome of the impetus given to venational study by his paper.
§ These Proceedings, xxxvii., p. 724, 1912.
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Stage 1.—Eschninae [Austrophlebia, Austroaeschna, Dendroaeschna, Eschna, Anax].

Stage 2.—Synthemini [Synthemis, Metathemis].

Stage 3.—Idocorduliini [Austrocordulia].

Stage 4.—Eucorduliini + Libellulinae [Hemicordulia, Orthetrum, Diplacodes; with Cordulephya a specialised offshoot from near the base of the Eucorduliini].

Let us now study these four stages in turn:

Stage 1.—Eschninae (Figs. 1-3, and Plate xi., figs. 1-3). All the genera studied under this stage, agree exactly, in the formation of their anal loops, with the description already given in the case of *Eschna brevistyla* (Figs. 1-3). In all cases, the basal side of the loop is A₂ and the proximal side is A₁, the latter fusing with Cu₁ for some distance, and finally turning inwards to complete the loop below.

Stage 2.—Synthemini (Figs. 5-8, and Plate xi., figs. 4-5). At first sight, there seems to be very little difference between the anal loop of the Synthemini and that of the Eschninae. But a little consideration will show us that those forces which culminate in the formation of the complex Italian loop are already at work. Two important changes are beginning to take place:

1. Ac bends off from Cu + A much closer to the base of the wing than to the triangle. [In Stage 1, it bends off somewhat nearer to the triangle than to the base, while in the Gomphinae it is still nearer to the triangle].

2. Consequently A₁ is stretched longitudinally, tends to decrease in diameter, and makes a weaker union with Cu₂.

Probably the larva of *Macromia* will be found to exhibit a similar arrangement, though we must not be too hasty in assuming a near relationship between this genus and the Synthemini. Metathemis agrees exactly with Synthemis.

This stage shows the first attempt to enlarge the basal area of the hindwing. It is carried out on very simple lines, viz., by a purely longitudinal stretching of the area between Ac and the triangle. Developed to its logical conclusion, it culminates in such forms as *Synthemis regina* ♂ and ♀, in which the enormously widened anal loop is split into two by the development of a straight supplement parallel to A₂ (Fig. 8, X); while, in the very broad-winged female, even A₃ is dragged in to make a third support, giving the insect an apparently three-portioned anal loop of immense width.
It is scarcely necessary now for me to say that these phylogenetic stages, taken from living examples, do not lie along one absolutely straight line of descent. Each, rather, lies a little off the direct line that culminates in the Italian loop; nevertheless, each is a true advance on the one before it.

**Stage 3.—Idocorduliini** (Figs. 9-10, and Plate xi., fig. 6). We now come to a stage exhibited by the rare larva of *Austrocordulia refracta* Tillyard, which stands, in my opinion, very nearly in the direct line of ascent to Stage 4. The line branched off from Stage 2 at a time when the area between Ac and the triangle, though tending to stretch more widely, was still only wide enough to support a loop of two cells' width. At this point, a new force came into play, viz., the beginning of a stretching transverse to the longitudinal axis of the wing. The combination of forces started that diagonal stretching which brought the Italian loop into being, and to which the slantwise-elongated cells of the hindwings of almost all *Libellulidae* bear irrefutable witness. *Not by growth of new wing-material, but by stretching out of the old, did this beautiful formation arise.*

**Fig. 9.**—*Austrocordulia refracta* Tillyard, 6. Tracheation of full-grown nymphal hindwing. (Stanwell Park, N.S.W.; Feb., 1914).

**Fig. 10.**—*Austrocordulia refracta* Tillyard, 6. Portion of imaginal venation, to show structure of anal loop. (Heathcote, N.S.W.; from a specimen, bred Dec. 20th, 1912).

We cannot omit, here, a reference to the behaviour of the hindwing-triangle. In Stage 2, that triangle was still distal from the arculus. Had it remained so, while Ac receded basad, the anal loop must inevitably have widened, and *Synthemis regina* might even to-day then stand as the apex of *Anisoptera* wing-development. But, as soon as the tendency to transverse stretching began, the hindwing-triangle followed the anal-crossing basad, and began to recede towards the arculus, until its basal side finally came to lie exactly under it. It is, indeed, curious to see how the necessity of *broadening* the hindwing should cause the triangle to recede and tend to broaden out *longitudinally*, while the almost equally insistent necessity for *narrowing* the forewing (to prevent overlapping on to the hindwing) should bring about an exactly opposite result, viz., the procession of the triangle away from the arculus, and an excessive broadening of it *transversely* to the wing-axis. In the case of the hindwing, the *pull* on the triangle stretched it longitudinally; while in the case of the forewing, the *push* on it, due to the rapid narrowing of the anal area, shut it up transversely like a collapsed framework, at the same time that it drove it away from the wing-base.

We are now in a position to understand Figs. 9-10. The shape of the area to be supplied by the anal trachea and its branches, has now altered so considerably, that we need not be surprised at the change in the relative importance of the various branches. As this area becomes elongated in a slantwise direction, A₂ becomes directly attached to Ac, and in this very favourable position, it begins to show a distinct gain in size and length compared with the other branches. Forming, as it now does, a kind of mid-channel along the whole anal area, it supplies the latter with the greater part of its oxygen. On the other hand, A₁, originally more important than A₂, now shows a further slight reduction from the form reached in Stage 2 (*Synthemis*). It still reaches Cu₃ just below its bifurcation from Cu₄, but is an exceedingly slender trachea, very small in comparison with Cu₄. It gives off slender branches inwards to help to form the separate cells of the loop, as far as the third set of cells from its base. But the rest of the loop, consisting of two more sets of
cells, is formed on its distal side by a strong descending branch of $\text{Cu}_{\text{a}}$, which we call $\text{Cu}_{\text{b}}$.

It is evident from this, that the elongation of the anal loop was first brought about by the inclusion of extra sets of cells beyond the original distal end still to be seen in Stage 2. If, in the loop of Synthemis (Fig. 7), we imagine the wing to be somewhat stretched in a slantwise direction so as to straighten out $\text{Cu}_{\text{a}}$, $A_{\text{a}}$ at the same time becoming straighter but not longer, while $A_{\text{a}}$ becomes both straighter and also considerably longer, we get an approach to Stage 3, which can then be completed by a basal narrowing and by the development of a strong $\text{Cu}_{\text{b}}$, distally. Hence we see that the loop of Austrocordulia is a composite structure, and no longer a true "anal loop," i.e., no longer enclosed purely between $A_{\text{a}}$ and $A_{\text{b}}$.

Further peculiarities in this area of the wing of Austrocordulia must here be noticed. Now that $A_{\text{a}}$ has obtained the commanding position under $A_{\text{c}}$, $A_{\text{b}}$ has shifted considerably basad, and become reduced in size. Hence arises the beginning of the decline of the anal triangle in the male—a movement which leads inevitably to the complete loss of the angulated wing, as seen in Hemicordulia and Libellulinae. Hence, in so far as the elongation of $A_{\text{a}}$ necessitates the reduction of $A_{\text{b}}$, so far may we say that the Italian loop is developed at the expense of the anal triangle. In Tetragnenurina (Needham, loc. cit., Fig. 19, p. 724) we see the maximum development possible to both at the same time; a development which may well be claimed to be the high-water mark of Anisopterous evolution, and from which the whole mass of the Libellulinae may be judged to stand on a lower level by regression, as they certainly do in powers of flight.

In Austrocordulia, the hindwing-triangle is greatly stretched out longitudinally, more so than in any other Libellulid, yet its basal side does not quite succeed in reaching the arculus. This excessive stretching, together with the extreme narrowing of the proximal part of the loop, are special to this genus, and are not to be judged as developments along the direct line between Stages 2 and 4.

Stage 4.—The final stage in the phylogenetic development of the anal trachea is to be seen in most of the Libellulinae and in the Eucorduliini (see Figs. 11-12, and Plate xi., figs. 7-9). Here $A_{\text{a}}$ has outdistanced all the other branches in development, and is to be seen as a very long and strong trachea running slantwise distad from $A_{\text{c}}$. As in the Eucordulinae, it still forms the basal
the posterior border or "sole" of the now stocking-shaped or Italian loop. The loop is still only two cells wide for the most part, but tends to widen at both ends, so that it is not unusual to find three or more cells in a row, both at the base and towards the tip. Finally, by the convergence of the distal ends of $A_2$ and $Cu_{as}$, an exceedingly elongated and pointed "foot" may be formed, such as is to be seen in Neurothemis (Needham, loc. cit., fig. 18, p. 724).

We have now to consider the formation of the midrib or symmetrical axis of the Italian loop. By reference to Fig. 11, it will at once be seen that this is not formed about a trachea at all. The midrib is, in fact, nothing more nor less than a cubital supplementary sector ($Cuspl$), formed on exactly the same lines (and even carrying, in Hemicordulia, the same mass of pigmentation) as $Mspl$ under $M_4$ and $Rspl$ under $Rs$, though attaining a far greater measure of usefulness owing to its fortunate position. In cases where the "toe" is not fully formed, as in Hemicordulia, this $Cuspl$ runs straight to within one cell's breadth of the "sole." But where there is a well-developed toe (e.g., in Diplacodes, Plate xi., fig. 9), it is cut off by yet another branch of $Cu$, about midway between its point of bifurcation from $Cu$ and its point of branching to give off $Cu_{as}$, and runs almost straight to the tip of the toe. Hence, in this extreme case, the midrib is formed chiefly by $Cuspl$; but its apical end, penetrating into the toe, is formed about the new branch from $Cu_{as}$.

Having now traced the development of the anal trachea through all its stages, we are in a position to give the true homologies of the much-discussed Italian loop. First of all, it is not an anal loop in the sense that the $Eschnine$ loop is, for it is formed as much from $Cu_4$ and its derivatives as it is from $A$. Of the branches of the latter, only $A_2$ enters into its composition. It is, strictly speaking, a cubito-anal loop, and should be designated as such, with the abbreviation $Cual$. The basal side of $Cual$ is in all cases $A_2$. Nearly always, it descends directly from $Ac$. But, in some genera, it may lie a little distal from or proximal to $Ac$. In all such cases, where larvae are obtainable, a strict study should be made, in order to discover any possible exceptions to the rule laid down; though such are not likely to occur, seeing that $A_2$ forms the basal side in all known forms throughout the series.

The distal side of $Cual$ is $Cu_4$. It is, therefore, not homologous with the distal side of the anal loop of the $Eschnine$, which is formed from $A_4$, or more strictly from the fusion of $A_2$ with $Cu_4$ for part of its length, and then from $A_2$ alone lower down.

The midrib of $Cual$ is a cubital supplement ($Cuspl$). It has no true homologue in any other subfamily. The straight supplement $X$, in Synthemis regina, is comparable to it, but is not its true homologue, since it is not formed by the fusion of small tracheal branches from $Cu_4$. The midrib is strictly analogous to $Rspl$ and $Mspl$, the sectors developed similarly under $Rs$ and $M_2$ respectively.

As regards the two rival theories, our investigations have, without doubt, proved the Theory of Double Descent to rest on an unsound basis, since it depended upon an incorrect interpretation of the homologies of the basal side and midrib of the Italian loop. On the other hand, the Theory of Single Descent is supported by the whole weight of the evidence obtained from the study of the nymphal wings.

Before passing on from the study of the anal loop, one more problem presents itself, viz., the question of the phylogeny of the reduced forms of the Libellulidae. Only one larva is obtainable, that of Cordulephya pygmaea Selys, a form in which the imago has an extremely reduced and narrowed hindwing, with an anal loop comprised by only two large cells. I have already indicated my belief* that this loop is a reduction from a more normal loop, and must be considered as a very highly specialised offshoot of the Encordulini. Let us now see what evidence is afforded by the nymphal wing.

Fig. 13 shows the anal area of this larval wing. The reduction from a considerably broader wing is very evident (as in the Zygoptera; see Plate xii., fig. 1) by the fact that the imaginal wing-border is drawn in, leaving a broad space below, into which

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* "On the genus Cordulephya," These Proceedings, 1911, xxxvi., p. 388.
DEVELOPMENT OF THE WING-VENATION OF ODONATA,

the fine ends of the tracheae penetrate for a very considerable distance. The same thing may be seen in the forewing of Hemi-
cordulia (Fig. 11A). What is of greater interest, however, is the
fact that, as in Stage 4, A₁ does not help to form the distal border
of the loop at all, but is a weak trachea curving in half-way
between Ac and Cu₁ to form the distal border of the first of the
two large cells forming the loop. A₂, on the other hand, is a
very strong, thick trachea, descending from Ac and forming the
basal side and part of the lower border of the loop. Cu₂ is
visible as a fairly strong trachea descending from Cu₁ into the
space below the imaginal wing-border. From these considera-

It is probable that the larval wings of all the narrow-winged
Libellulinae would yield similar evidence of descent from broader-
winged forms. None of the larvae are, however, at present
obtainable. But in the exuviae of Nannophlebia and Lathrecista,
which I have seen, the breadth of the hind wing-case certainly
suggests a descent from a broader-winged form.

The foregoing discussion has been confined to the hindwings.
The forewings of the Anisoptera are not, however, without
interest. First of all, we notice the absence of pigmentation
throughout the posterior longitudinal portion of the wing-case,
due to the fact that the hind wing-case overlaps the forewing to
that extent (see Plate xi., fig. 8). This may well be a contribut-
ing cause to the narrowing of the anal area, since absence of
light means absence of pigmentation, and pigmentation precedes
the development of the permanent venation. [Contrast the de-
velopment of the wings of Ephemeridae, in which the fore wing-
case overlaps the hind, and the forewing far outruns the hind in
development].

Secondly, changes take place as we pass from stage to stage,
although these changes are small compared with those in the
hindwing.

In Stage 1 (Eochinae), the four typical branches of A are
present, and placed in the primitive positions. A₁ reaches and
fuses with Cu₁ and keeps this position through all succeeding
stages.

In Stage 2 (Synthemini), the final development of A₁ is already
almost accomplished. Stage 3 being very similar to Stage 2, we
may study the forewings of these two stages together. We
then notice the following advance from Stage 1.

As in the hindwing, Ac has come to be much closer to the
wing-base, while A₂ has become hitched to A₁. A₂ keeps its
original position somewhat distad from Ac, while A₁ is greatly
lengthened out, and consequently gives off supplementary tracheae
downwards to supply the elongated area below it. Owing to the
compression of the triangle (explained above), which is already,
considerably advanced in Synthemis, though not so evident in
Austrocordulia, A₁ takes a bend slightly downwards (Plate xi.
so as to meet Cu₂ just at its point of greatest curvature. Thus A₁ and Cu₂ between them, form two sides of a large triangular space, the subtriangle (st). One of the set of cross-veins developed transversely between Cu₁₂ and A₁ now becomes specialised by slantwise lengthening, so as to run from the first bend of Cu₁₂ towards the bend of A₁, and thus develops into a firm support for both bends, as the inner side of the subtriangle. In Austrocordulia, owing to the small amount of transverse elongation of the triangle, st is rather small, and consists of one strongly-formed triangular cell. But in Synthemis, owing to further transverse elongation of the triangle, st has increased very much in area. Hence is developed the system of supporting cross-veins, which divides the subtriangle into three cells, and which persists throughout the rest of the phylogenetic series with only slight variations.

Stage 4 (Eucorduliini and Libellulinae) shows very little advance from Synthemis. The growth of A₁ is stronger, the bend much sharper (approaching a right angle), the subtriangle larger and more strongly formed, but essentially of the same structure (Fig.11A). It tends, however, to become four-sided through a second bending of A₁, and at this same point A₁ gives off a fairly strong branch, which runs at first considerably basad, then bends completely round, and finally runs distad to meet A₁ itself after its "break-back" from Cu₂. Thus there is formed a small and complete "anal loop," represented in the imaginal venation by two strong supporting cells lying under st.

In Plate xi., fig.13, the very interesting forewing of Cordulephya nymph is figured. It shows several peculiarities. Ac runs very slantingly, parallel to the basal side of the triangle. The bridge-vein is extremely well developed. The postnodal area of the wing is excessively shortened, and the tip of the wing is formed irregularly, as if a small part of the margin had been broken off. This last peculiarity is to be seen also in Hemicordulia, and probably in other Eucorduliini, while the shortening of the postnodal area is also noticeable in this group. These are two further links in the chain of evidence which binds Cordulephya to the Eucorduliini.

In Synthemis, the hindwing of the larva outgrows the forewing very much more than in other genera. This may be due to the diverging position of the wing-cases, which do not lie parallel along the back of the insect, but resemble those of Cordulegaster. Such a position must be regarded as a specialisation connected with the form and habits of the larva. In a nearly full-grown nymph of S. macrostigma, I found the forewing to be only slightly more than half as long as the hindwing.

Having now completed the study of the anal loop, let us turn our attention to the Gomphinae, where no loop is formed, and study the anal area there. The only genus available to me was Austrogomphus. There are, however, two distinct types of larvae included in this genus. A. ochraceus Selys, and A. heteroclitus Selys, represent these two types. As will be seen from Figs.15-16, the tracheation of the anal region shows considerable differences in the two types.

In A. ochraceus (Fig.15), the anal trachea, at the end of Ac, branches into three. The branch running basad is A₁ₗ and from it the secondary anal vein A' is developed as a bridge-vein. The branch descending directly from Ac is almost certainly A₁, since it forms the distal side of the anal triangle in the male. The branch running distad represents A₁₂, but does not reach Cu₂ at any point. This branch divides into two rather low down. These two branches may be A₁ and A₁, respectively, but their determination is doubtful.

In A. heteroclitus (Fig.16), the anal trachea, at the end of Ac, branches as usual into two. The branch running basad is A₁ₗ. A₁ descends from A₁ somewhat basad from Ac, and forms the distal side of the anal triangle of the male. The branch running distad represents A₁₂, but does not reach Cu₂ at any point. This branch divides into two rather low down. These two branches may be A₁ and A₁, respectively, but their determination is doubtful.
sharply downwards, and runs to the wing-border. A small trachea from Cu, meets it a little below this final bend (Fig.16, and Plate xi., fig.12).

We see from this that the anal trachea is more primitive in the Gomphinae than in the groups already discussed, in so far as A, does not at any point reach Cu, or fuse with it. Hence no anal loop comparable to that in the Eschninae or Libellulidae can be formed. In this connection, it is to be hoped that the anal tracheation of such forms as Hagenius (Fig.19) will be worked out by those who have access to them. The small loop there formed may quite probably be enclosed between A, as the upper part of its basal side, A, as the lower part of its basal side, Cu, as the upper part of its distal side, and the small branch-trachea from Cu, (shown in A. heteroclitus) completing its distal side lower down and joining A,. In that case, the correct notation for the wing-veins will be that given in Fig.19. The "anal loop" of Hagenius, under these circumstances, is not homologous, in any sense, with the anal loops of the other groups, but is more of the nature of a subtriangle.

The point cannot, however, be settled without a study of the larval wing-tracheation.

If my interpretation of the branchings of A in the Gomphinae be correct, Needham's notation for that subfamily will need altering. In his figure for Gomphus descriptus (loc. cit., p.708), A, and A, remain as indicated, but the vein labelled A, must be altered to Cu, (= proximal branching of Cu,). His figure on p.707 also shows that this is so. Probably A, forms the greater part of the weak zigzag vein descending between A, and Cu, and arising from A, one cell below the subtriangle.

It is very necessary that other genera of Gomphinae should be studied in this manner. A satisfactory classification of this subfamily has not yet been attained, but a study of the larval wing-tracheation would go far towards establishing it, and would, in any case, reveal any hidden convergences which may be lurking.
to catch the systematist who pins his faith to imaginal wing-venation only. That such may be reasonably expected to occur, will be seen by perusing Section B of this part, in which a most unexpected and extraordinarily well hidden convergence is brought to light in the Agrionidae.

To return to Austrogomphus, it is now necessary to propose a subdivision of this genus into two, as follows:

(1.) Distal side of anal triangle in the male descending perpendicularly from Ac (Fig. 17). Larva with flattened abdomen, four-jointed antennae only moderately swollen, and rectal tracheal gills without papillae. Larva lives in trash in running streams.

Genus Austrogomphus.

Type, Austrogomphus guerini Ramb.

This genus includes, most probably, all the species at present grouped under the name Austrogomphus, except the three separated out below.

(2.) Distal side of anal triangle in the male descending from A' before the level of Ac, and running in a slanting curve away from it (Fig. 18). Larva with rounded abdomen, four-jointed antennae (in which the third joint is greatly swollen and rounded, while the fourth joint is practically obsolete), and rectal tracheal gills with numerous papillae. Larva lives completely buried in clean sand in running streams.

Genus Hemigomphus Selys (re-defined*).

Type, Austrogomphus heteroclitus Selys.

This genus, which corresponds to the second division of de Selys' suppressed genus Hemigomphus, includes only three species, viz., A. heteroclitus Selys, A. comitatus Tillyard, and A. armiger Tillyard.

Hemigomphus is, almost certainly, an offshoot from the Palearctic Onychogomphus-group, with which it agrees in the form of its larval antennae and rectal gills. It has, however, suffered considerable reduction during its migration eastwards. It may, in fact, be considered as very probably a specialised offshoot from the Oriental genus Burmagomphus, and its arrival in Australia is almost certainly much more recent than that of Austrogomphus, s.str.

As for the latter, its origin seems lost in the mists of antiquity, since no other Gomphinae are, so far, known in which the larval rectal gills have not developed papillae. Both genera must have entered Australia from the North-West by way of Timor, since no Gomphinae occur in the Papuan subregion.

Needham's supposition, that A₁ may possibly be aborted in the Gomphinae, seems to me to be unlikely. For, in the more primitive forms, it is just this particular branch of A which shows the greatest development. It seems rather that we have to do with forms in which A₂ is very poorly developed, this being due to the fact that the failure of A₁ to reach Cuₙ left only a very small area between A₁ and A₂, for A₃ to supply.

Having now followed the development of the anal trachea in both fore and hind wings through all its phylogenetic stages, we may conclude this section by giving a table of the principal differences between the Comstock-Needham notation and the new notation here adopted:

<table>
<thead>
<tr>
<th>Main longitudinal veins at base of wing</th>
<th>Comstock-Needham Notation</th>
<th>New Notation</th>
</tr>
</thead>
<tbody>
<tr>
<td>First</td>
<td>C</td>
<td>C</td>
</tr>
<tr>
<td>Second</td>
<td>C₄</td>
<td>C₄</td>
</tr>
<tr>
<td>Third</td>
<td>R₄</td>
<td>R₄</td>
</tr>
<tr>
<td>Fourth</td>
<td>Cu₄</td>
<td>Cu₄</td>
</tr>
<tr>
<td>Fifth</td>
<td>A₄</td>
<td>A₄</td>
</tr>
<tr>
<td>Italian loop of Libellulidae:</td>
<td>A₃(Ris)</td>
<td>A₃</td>
</tr>
<tr>
<td>Basal side</td>
<td>A₃(Ris)</td>
<td>A₃(Ris)</td>
</tr>
<tr>
<td>Distal side</td>
<td>Cu₉</td>
<td>Cu₉</td>
</tr>
<tr>
<td>Sole of foot</td>
<td>?</td>
<td>?</td>
</tr>
</tbody>
</table>

Note on the so-called “First Postcubital.”—In Plate xi., fig. 3, I have shown the tracheation of the hindwing of the nymph of...
**Development of the Wing-Venation of Odonata.**

Dendroaeschna conspersa Tillyard, the only nymph so far studied of an *Eschnine* with reticulated basilar space. This shows the interesting fact that the anal-crossing Ac is *not* the first postcubital cross-vein, but the second, since there is one cross-vein developed between it and the base. In the imaginal wing, at first sight, the whole series of four (sometimes five) postcubitals appears very similar, except that the last is placed slantwise to form a weak subtriangle. But a little examination shows us that the second postcubital is also slightly bent, and very slightly thicker than the others. The reduction in strength from the strong trachea Ac to the weak cross-vein is, of course, exactly on a level with the formation of the "oblique vein" treated of in the next section of this paper. But here, the obliquity of the trachea was never very great, and is practically lost in the imaginal cross-vein.

We see from this how very inconvenient, and even incorrect, the term "first cubito-anal cross-vein" may become. It should certainly be done away with once and for all, and the term "anal-crossing" (Ac) be substituted. In the closely veined species of *Eschninae*, there should never be any difficulty in picking Ac out, since it is always the cross-vein lying slightly distad from the distal side of the anal triangle of the male. Hence, in *Basieschna* and *Boyeria*, for instance, it is actually the first cross-vein, in spite of their archaic reticulation.

**Section B.—The occurrence of a bridge-vein in Zygoptera.**

Needham states that a true bridge-vein is not formed in any of the *Zygoptera* except the Lestine. In that subfamily (Plate xii., figs.3-4), it is very easily discovered in the nymphal wing, and agrees entirely in its form with the bridge-vein of *Anisoptera*, except for its greater length. In the imaginal wing (Plate xii., fig.4), it carries Rs backwards in a straight line, to attach to M₂ very slightly distad from the origin of M₃.

The occurrence of this bridge-vein in the Lestine must be of very great phylogenetic importance, since it almost certainly indicates a separate line of descent for that subfamily, as compared with the non-bridgeveined *Zygoptera*. We should, therefore, search carefully for any evidence still existing as to what this line of descent was like, and also try to discover whether any other *Zygoptera* exhibit a bridge-vein.

Now in the very remarkable dragonfly, *Epiophlebia superstes* Selys, whose wings are figured by Needham (loc. cit., Plate xii., fig.3), a typically Lestine bridge, with clearly indicated oblique vein, can easily be made out; and will, I feel sure, readily be recognised and accepted by all students of *Odonata* without requiring corroborative evidence from the larval wing, which will probably never be found, even if the dragonfly be not already extinct. The remarkable and isolated wing-type shown by *Epiophlebia* has so many points of Lestine affinity, that it may well be claimed to lie on the direct line of descent of that genus. The chief difference lies in the much greater reduction of the Lestine wing, and the departure of M₂ from M₁ far distad from the subnodus. The latter is, however, a characteristic of all highly reduced *Zygopterid* wings, and must be considered as a specialisation brought about by the shifting of the nodus basad. The trachea M₂ need not follow the subnodus towards the base, since it is not really connected in any way whatever with either Sc or R, and its function is to supply the middle portion of the apical part of the developing wing. The genus *Archilestes* shows an intermediate position of M₂.

In quite another direction, *Epiophlebia* shows strong relationship to the *Anisoptera*, particularly to the Gomphinae. In the larger *Gomphinae*, the oblique vein is placed about as far distad from the subnodus as it is in *Epiophlebia*, and the bridge itself is almost, if not quite, as long. Furthermore, in both, M₂ descends from the subnodus, and there are two thickened anastomosing antenodals of flat triangular form. Finally, apart from its wing-venation, *Epiophlebia* is characteristically *Gomphine* in the short build of its body-parts, in the large size and closeness of the eyes in the male, and its archaic bicolorous (hylochrome) colour-pattern.

We stand here, in fact, almost on the verge of the first dichotomy between *Anisopterid* and *Zygopterid* forms. It needs but a single cross-vein inserted into the quadrilateral of the hindwing of *Epiophlebia* to turn that cell into a weak "supertriangle-
triangle of early Anisopterid type. The greater breadth of the hindwing is, in itself, evidence of a descent from Anisopterous ancestors; while the fact, that the forewing-quadrilateral is already of Lestine form, strongly suggests that the latter group are highly reduced descendants of an originally weakly-triangled Anisopterous stock. In that case, the sharply acute distal angle of the quadrilateral is the last remaining piece of evidence of the originally present triangle. It does not follow, of course, that any of the Zygoptera which possess fairly regular quadrilaterals were descended from similar ancestors; in fact, the regularity of the quadrilateral is an almost certain sign that all these forms branched off as reduced members from the main stock long before the first beginnings of the formation of the Anisopterid triangle. On this view, the Calopterygidae and their more highly reduced descendants, such as the Podagrionini, are a far more archaic stock than the Epiphelebia-Lestes line, which has a truly Anisopterous ancestry. As regards the acutely-angled quadrilateral of the Agrionini, we should hesitate to describe that also as the result of a reduction from an early Anisopterous form, since we have, at present, no other evidence in favour of that view, and a good deal against it. It is probably much more truly a specialisation of an originally regular quadrilateral.

To turn now to our second point—can we indicate any other Zygopterous forms which possess a bridge and oblique vein? A search through the whole series of known imaginal wings will not reveal a single case with certainty; hence we must turn to the study of the larval wing. Now there is, in Australia, a genus (Synlestes) which is usually placed in the Podagrionini with Argiolestes and its allies. I have, for years, been struck by the similarity in habits, appearance, and, in particular, larval form, between Synlestes and Lestes, and also by the wide divergence in all points (except wing-venation) between Synlestes and Argiolestes. I, therefore, expected that the similarity in wing-venation between these two genera must be due to convergence. This year, I obtained nearly full-fed larvae of Synlestes weyersi, Argiolestes griseus, and A. interomelas, and photographed the larval wings. The result was even more astonishing than I had expected, as will be seen by comparing Plate xii., figs. 5-8, also Plate xiii., figs. 2-3. While Argiolestes shows a typical Zygopterid tracheation, with no sign whatever of either bridge or oblique vein, Synlestes exhibits a very long bridge, which would have appeared as of typical Lestine form, had it not become very cleverly masked, in the imago, by becoming hitched on to M, close to its origin, instead of joining up to M, in the usual manner. Also, it is very remarkable to see that, in spite of the excessive obliquity of trachea Rs at its crossing from M,, the corresponding cross-vein in the imago is so little oblique in direction (Plate xii., fig. 6, o) that nobody would notice it at all unless he had the larval wing to guide him. In fact, from my long series of Synlestes weyersi, I can select a fair number of specimens in which the obliquity of this vein is completely lost. To such unprecedented lengths, then, can convergences go, in the formation of apparently similar and closely allied types of imaginal wing-venation, that we can now lay down only one safe rule for the study of the phylogeny of the Zygoptera; that is—Never be sure of the homologies of the parts, in any genus of Zygoptera, until you have studied the tracheation of the larval wing.

Having thus shown that Synlestes has no real affinity to the Podagrionini, towards which group it is a pure and very cleverly masked convergence, we must next enquire whether any other genera, now included in that tribe, ought to be taken out and placed with Synlestes. To this, bearing in mind the rule I have just laid down, we must give a very guarded reply. Without having seen even the insect itself, and simply from the photographs of wing-venation sent to me by my friend, Dr. F. Ris, I am able to state my very strong conviction that the genus Chlorolestes will be found, when its larval wings are examined, to possess a bridge and oblique vein of exactly similar form to those of Synlestes. In the imaginal wing, the oblique vein can be detected some four to six cells distad from the bifurcation of M, from M,, much more clearly than it can be usually seen in Synlestes itself. Chlorolestes, like Synlestes, has the distal angle of its quadrilateral very acute, and Cu, in both genera arches strongly upward away from Cu.
In the fossil genus, *Heterophlebia*, about which unfortunately very little is known, there is an attachment of what is probably a long bridge-vein to M, in the manner of *Synlestes*. It is quite probable that this fossil stands in somewhat the same relationship to *Synlestes* that *Epiophlebia* does to *Lestes*. A careful study of the hindwing-quadrilateral of *Heterophlebia* should go far towards completing the proof of the *Anisopterous* ancestry of this group.

It will be seen that the above study affords us a very satisfactory point from which to start on an entirely new classification of the *Zygoptera*. This will be somewhat more fully dealt with in the next section.

Section C.—The general tracheation of the larval wing in *Zygoptera*, and its homologies with that of the *Anisoptera*.

I have already indicated that my study of the general tracheation in *Zygoptera* is necessarily incomplete, since it is confined to the *Agrionidae*. However, in that family I have been able to obtain and study a large number of different genera, a list of which is here given:

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<tr>
<th>Tribe</th>
<th>Genus</th>
<th>Species</th>
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<tbody>
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<td><em>Synlestes</em></td>
<td><em>S. weyersi</em> Selys.</td>
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</tr>
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<td><em>Neosticta</em></td>
<td><em>N. canescens</em> Tillyard.</td>
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<td><em>C. billinghamvari</em> Martin.</td>
</tr>
<tr>
<td></td>
<td><em>Austrolestes</em></td>
<td><em>A. cyanus</em> Selys.</td>
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</tbody>
</table>

The list thus comprises nine genera, selected from five tribes, and represents practically all the *Agrionid* larvae obtainable within one hundred miles of Sydney. Several of them, indeed, are very rare, and only to be obtained by thorough searching of special localities.

In carrying out this research, one of the principal difficulties was found to be the extreme thinness of the wing-cases, through which the slightest pressure served to disarrange the tracheae. Many specimens were spoiled through this. The plan which I finally adopted was to dissect off the two wings of one side together, under water, with a fairly large portion of the pleural attachment; then, to separate the two wings by a sharp cut in the plane of the wing-case, not transverse to it, so as to cut the attachment in halves without exerting any pressure on the wing-cases themselves; and, finally, to float each wing out separately on to a slide with plenty of water, lay down a cover-glass gently on to it, and photograph it while still in the water. If desired, the attachment can be cut completely away in order to obtain a planar surface for focussing; but as this usually pulls the delicate anal tracheae away from its attachment to Cu, it should only be done for enlarged studies of other parts of the tracheation, as for instance, the studies of the bridge (Section B, above).

Another great difficulty is the fact that some larvae have very hairy wing-cases, while many have them very deeply pigmented. The wing-cases of *Argiolestes* are very hairy and rather thick; those of *Isosticta* nearly always jet black. Some ingenuity is required in manipulating these insects. Remembering that the dark colour of these larvae is mainly due to their being bottom-dwellers, I placed some *Argiolestes* and *Isosticta* larvae in a jar with a mass of water-weed alone, no sandy bottom being supplied. After wandering round the glass bottom for some time, most of the larvae took to the water-weed, on which they rested clumsily with outspread legs (showing their inability to cling closely in the way that habitual weed-dwellers do). One *Argiolestes* and several *Isosticta* larvae went through an ecdysis in this position; and instead of rapidly darkening, as they usually do, remained pale brownish for many days, showing even a tinge of green also. This was what I expected. From these larvae, I obtained very fair photographic results, from which the diagrams (Plate xii., figs. 7, 11) have been taken. I also obtained a photograph of an *Isosticta* larval wing soon after ecdysis, and was interested to notice that all the imaginal wing-venation showed...
up white and unpigmented, with large patches of black pigment in each separate cell.

For our general study, I will now select the largest as well as the palest of all the larvae examined, that of Caliagrion billinghursti Martin. This very beautiful larva is of a bright green colour, and its wings are pigmented uniformly and lightly all over. I was, unfortunately, unable to study any of the earlier stages of this or any other larva, owing to the lateness of the season when I first started (September). A complete study of the Caliagrion nymph will, I hope, be undertaken next season, with a view to determining the ontogenetic development of Rs.

A very clear photograph of the complete hindwing is given in Plate xi., fig.14, while Fig.1 of Plate xiii., gives a much more highly magnified photograph of the most important parts. From these and from the diagram in Plate xii., fig.1, it will be seen that, in Caliagrion, as in all the Anisoptera, trachea A fuses with Cu as far as the anal crossing (Ac). This can also be seen very clearly in Austrolestes, less clearly in Symlestes; while, in the smaller species, it is often very difficult to detect any trace of A at all. This is especially the case with the Protoneurini, Neo- sticta, and Isosticta, in which the whole anal trachea seems to be quite aborted, except that, in one or two specimens, I have detected a very fine and short basal portion which fails to reach Cu. However, in all cases Ac can be detected, though not without careful searching in the case of the most reduced forms.

From this, we must conclude that the anal trachea of the Zygopterid nymphal wing behaves in the same manner as the corresponding trachea in Anisoptera. Hence, as far as A' and Ac are concerned, the new notation applies to all Odonata.

The next point is a very startling one, viz., that Caliagrion is a reduced descendant from an original ancestor which had a fairly broad anal area supplied by a well developed four-branched anal trachea. Also, since a difference in the width of this anal area, and in the amount of development of the four branches of A, is still easily to be detected in the fore and hind wings of the Caliagrion nymph, we must go further, and state that this ancestor was of an Anisoptera type; not, of course, necessarily with triangles developed, but most certainly with hindwings broader than forewings.

Further proof of this interesting point can be obtained by studying the formation of the imaginal venation in the nymph of Caliagrion. The original posterior border of the wing is formed at first, in the usual manner, as a pale band running far posteriorly to Ac, towards which the remnants of two descending veins can still be seen developing as thin white bands along A2 and A3 respectively. Further, the white bands which descend from Cu to the posterior border, are not only strong and clearly to be seen, but they are of great length compared with their remnants in the imago. In fact, the whole of this portion of the wing is constrained to pass through, in its ontogenetic development, the past phylogenetic stages of its ancestry, before arriving at its present highly specialised petiolate form. Just in this case, the application of the Biogenetic Law of Haeckel seems very complete and exact.

As metamorphosis approaches, the wing-rudiment becomes drawn away, along its posterior margin, from the edge of the wing-case; it shrinks in rapidly, but more especially towards the
base, where it finally coalesces with A' from the base to Ac. Beyond Ac, it takes a slanting direction from Ac towards Cu_{3b}, which is now only about half its original length; all the other subcubital cross-veins becoming similarly shortened. A similar, but less intense narrowing also takes place along the costal border. As a result, the base of the wing becomes quickly narrowed to less than half its former width, and, in this shape, it is withdrawn from the wing-case at metamorphosis. The expansion which follows mainly affects the "blade" of the wing, the petiolate stalk undergoing a comparatively small lengthening.

A further point of interest in Zygopterid wings is the development of Cu. In all Zygopterid wings, there is very little curving of this trachea. In some cases (as in Calagrion), Cu_{3} continues the line of Cu_{3b} while, in others, it is about as much curved as Cu_{3}, but, of course, in an opposite direction (see Synlestes, Plate xii., fig.5). In every case, Cu_{3} is less strongly developed than Cu_{3}, the latter being a very strong and almost straight trachea. In the Protoneurini, Cu_{3} undergoes a gradual reduction, until, in the most asthenogenetic forms (Plate xii., figs.9-12), it is seen to be only a very short trachea terminating somewhere about the level of the origin of M_{2} from M_{1}. Its length varies very much in the different genera. In many genera, Cu_{3} is completely suppressed, and Cu then appears as a short, unforked trachea, slightly bent downwards under the arculus. In such forms, it is not surprising to observe the complete disappearance of trachea A, except perhaps for a minute basal portion not easily observed; since the asthenogenetic tendency must affect A before it can touch Cu_{3}.

These highly specialised Protoneurini are, without doubt, from the point of view of the reduction of their tracheal system, the most advanced members of that very prolific and successful phylogenetic line, which probably includes, in the form of numerous more or less successful side-branches, the whole mass of the Calopterygidae, and also all the Agrionidae possessing regular quadrilaterals.

Let us now pass to the question of the origion of Rs in Zygoptera. In all except one of the forms so far examined, no connec-

tion can be detected between Rs and R, but Rs in all these cases appears as a branch of M. It can generally be detected by its peculiar method of parting from M, which is at a considerably greater angle than that made by a true branch of M, such as M_{3} (Plate xii., fig.1). This distinct curve in Rs, on leaving M, is most probably due to the original manner in which it cut across and under M_{1} and M_{2}, before it became permanently hitched on to M_{1}. As Needham has justly observed, there can be no difficulty in understanding this cutting-off of Rs from R, and its subsequent permanent attachment to M. For with the setting-in of the asthenogenetic process, and the consequent narrowing of the wing-rudiment in width, any difference of level which originally existed between M and R (and the fact that Rs still passes under M_{1} in Aesoptera shows that there was once a difference in the level) must inevitably become lessened. Thus the trachea Rs must gradually become pressed near its base by the stronger overlying M_{1}, and if it could not effect a union with the latter by the abortion of its original base, it would inevitably perish for lack of oxygen.

Let us now examine the condition seen in the Protoneurini. The arrangement of tracheas in the region below the nodus seems to be the same in Isosticta (Plate xii., figs.11-12) as it is in Calagrion. Two trachea branch off from M_{1}, close together. One would naturally suppose that the more proximal of these is M_{3} and the more distal is Rs, as labelled in the plate (with a query). But if we turn to the closely allied genus Neosticta (Plate xii., figs.9-10), we find Rs actually descending from R below the nodus, and crossing both M_{1} and M_{2}. Having done so, it runs along only for a very short distance, and then ends up; so that the rest of the imaginal vein Rs is not found about a trachea at all.

It seems very probable that we have, in Neosticta, the condition described above, viz., that Rs has failed to connect basally on to M, and is in process of perishing for lack of oxygen, owing to pressure from the overlying branches of M. If this is really so, then we might well consider that Isosticta shows the next step in advance, viz., that Rs has attained a basal fusion with M,
and hence gets a plentiful supply of oxygen, and grows to its full length. In that case, we must transpose the lettering in the plate, and name the more proximal trachea Rs.

If we accept the above solution, the Protoneurini (so far as known) will differ from all other Agrionidae in having Rs crossed under three branches of the nodus instead of two. The question, however, should not be regarded as finally settled, since it is only fair to point out that the wing of Neosticta is so highly pigmented, and the trachea Rs so faintly indicated, that I may have made a mistake in my interpretation of its course. In Plate xiii., fig.4, I give the actual photograph itself, but I may add that the wing itself, when first examined, was somewhat clearer than the photograph, and gave me a distinct impression of Rs crossing under M 3 as well as M 1 .2. The point can only be finally settled by further investigations, if possible on larvae fresh from an ecdysis, at a time when pigmentation is less dense.

Concerning the rest of the Zygopterid nymphal wing, there is very little of interest. The arculus is formed exactly as in Anisoptera by M descending from R, but the supporting vein formed underneath it, and completing it, also forms, of course, the basal or proximal side of the quadrilateral. The distal side of this latter is another cross-vein connecting M 3 with Cu at its point of bifurcation. The subcosta is a very weak trachea, and takes very little part in forming the nodus, which is here constructed from a small thick trachea arising from R, but principally by a simple vein, devoid of tracheae, and blocked off by a huge mass of pigment proximally. This formation is an asthenogenetic specialisation derived from the older method shown in Anisoptera (where Sc plays the principal part), and is due to the weakening of Sc, caused by the narrowing of the wing.

All the wings studied under the tribe Agrionini agree with Calinigrion in all essential particulars, except that Ac and its branches are not so clearly to be seen as in the larger larva. The distribution of tracheae in Argiolestes is also essentially similar to that in Calinigrion, the chief difference being that, in the latter, all tracheae run nearly parallel or slightly converging, while in the former, the wing being broader apically, they tend to diverge and allow of the introduction of short supplementary sectors (Plate xii., fig.7). As in Anisoptera, forewings can be distin-
guished from hindwings easily by the fact that they are only heavily pigmented from the costal border to M 1 . All the rest of the wing, being covered by the hindwing, is pale and very little pigmented. The erect position of the wing-cases, seen in adult Zygopterid larva, is only assumed after the last ecdysis, at a period shortly before the final metamorphosis. Anisoptera behave in the same way, but the change is perhaps not so noticeable.

For general study, forewings may be preferred to hindwings, since they yield much clearer photographs. But for the study of the anal trachea, the hindwing should be selected, since it is broader at the base, and shows the four-branched condition much more clearly.

Much more remains to be done in the study of the nymphal wings of this interesting Suborder. The present research is only a bare beginning, on which, it is to be hoped, other investigators will be able to build. Particularly in the Calopterygidae must careful study be made of all possible nymphal wings; for it is just amongst these archaic end-twigs that we may expect to find the missing steps in the development of Rs across M, and in the reduction of the anal trachea.

We may profitably conclude this section by a short discussion on the question of the classification of the Suborder Zygoptera.

It becomes now more than ever apparent that the Selysian division into Calopterygidae and Agrionidae is quite untenable as a natural dichotomy. More than this, it is pretty clear also that the Zygoptera are not, like the Anisoptera, derived from any original pure line of descent. Triangle-formation most certainly only started once; and, however far back new fossil discoveries may take us as regards the first formation of the triangle, there can be no doubt about the origin of all Anisoptera from that single line of descent, which Paleontology already places as far back as the Trias, and which probably began in the Permian period. Most of the Zygoptera (certainly all those with regular quadrilaterals) must have branched away from the Anisoptera-line before this. But who can tell how many separate branch-
ings took place, even amongst this one portion of the Suborder? The origin of the tribe Agrionina is doubtful, for their acute quadrilateral might yet be proved to be the reduced remnant of an originally weak Anisopterid triangle-formation. Finally, standing out clearly from all the rest as the most recent offshoot from the Anisopterid line, we see the Epiplophlebia-Synlestes-Lestes line of descent, which branched off from that line not very far from the beginnings of the Gomphinae, and whose sharply angular quadrilateral is almost certainly an Anisopterid remnant.

Were it not for the problematical position of the Agrionina, which form the greater number of the Zygoptera, and must, therefore, be satisfactorily placed in any classification that is to be of any use, we might see the dividing line in the form of the quadrilateral. Our two main groups would then be the Zygoptera Rectangularia, with more or less regular quadrilateral, and the Zygoptera Acuta with the distal angle of the quadrilateral sharply acute. But this division is most probably scarcely less unnatural than the Selysian. It would, therefore, be unwise to press for its recognition as a natural basis for classification. On the other hand, just as the terms Calopterygidae and Agrionidae, though indicating admittedly unnatural groups, do carry a certain value as the names of groups possessing a single character common to every member of each (at least, with few exceptions)—and are, therefore, of great value to students not very familiar with the intricacies of Odonate wing-venation—so also, I would urge a loose acceptance of the terms proposed, on the ground that they may prove of very great benefit in subsequent phylogenetic discussions.

The time is not yet ripe for making more than a beginning at the difficult problem in hand. That beginning I now make by selecting the Epiplophlebia-Synlestes-Lestes line of descent as a single pure line, descending from the main Anisopterid stock at a later period than any of the other Zygoptera. These, I consider to be worthy of family-rank at least; hence I propose, for them, the family-name Lestidae, with the following definition and subdivisions:

**Family Lestidae.**

Quadrilaterals of all four wings, but especially of forewings, with their distal angle very acute. Rs leaving M 2 considerably distad from subnodus. A long bridge-vein developed backwards from Rs towards the bifurcation of M 1 2 from M. Excluding fossil forms, three subfamilies may now be proposed under the above heading:

1. Bridge connecting with M 1 2
2. Bridge connecting with M 1
3. More than two antenodals, of which two are thickened.

**Subfamily 1. Epiplophlebiinae.**

Only two antenodals (rarely three). Slender petiolate wings. M 2 departing more or less distad from nodus. General facies of normal Zygopterid form.

**Subfamily 2. Synlestinae.**


**Subfamily 3. Lestinae.**

Mere robust forms with many antenodals [Fossils only. Subfamily Heterophlebiinae].

Of these, the subfamily Epiplophlebiinae contains the single genus Epiplophlebia Calvert (= Paleophlebia of Selys). The subfamily Heterophlebiinae contains only the single fossil genus Heterophlebia, which has not yet been fully studied. The subfamily Synlestinae contains the genus Synlestes, Chlorolestes, and possibly other additions from the ranks of our present tribe Podagriinae. The subfamily Lestinae remains exactly as at present recognised, with Archilestes as its most archaic genus (M 2 fairly close to subnodus) and Australolestes as its most reduced, and probably most caenogenetic development.

There can be little doubt that the tangle of forms left over, after the extraction of the homogeneous Lestidae, will eventually be unravelled by scientific treatment. But the problem calls for not months but years of research. The point of division must be looked for still in the behaviour of Rs, since there are probably, in the Calopterygidae, a number of archaic forms in which
Rs never succeeded in getting under more than the first branch (M₁) of the median trachea. Forms like Diphlebia, which show a peculiar oblique vein under M₁ far distal from the subnodus, need also a thorough investigation; since in such cases the vein, at present taken to be M₂, may eventually prove to be none other than Rs itself. There, for the present, we must be content to stop, resting in the certainty that the many forms of Calopterygidae larval wings will one day yield a wonderful harvest to the fortunate student who has a chance of investigating them.

Part ii.

The study of the source of the Oxygen-supply of the Wing-tracheae.

Section A.—Description of the tracheal system of the thorax.

The tracheal system of the thorax can only be studied in Anisoptera by means of very careful dissections, or by serial sections. Dissection is difficult, owing to the great thickness of the pleural ridges and their underlying muscles, in which it is very difficult to follow the course of the alar trunk. Eight larvae of Enarsche were dissected, but the complete result was obtained only by piecing together the separate points made out in different larvae.

The most satisfactory method of study is to select a Zygopterid larva immediately after its final larval ecdysis, and study it directly, under a low power of the microscope. If a green or yellow transparent larva be chosen (Lestes, Ischnura, or Calagrion) and submitted to strong transmitted light, the whole tracheal system stands up clearly in black, against a background of transparent pale greenish or yellowish.

The following description embodies the general results obtained for both Anisoptera and Zygoptera.

In all the specimens examined, the great dorsal trunks pass into the thorax from the abdomen with an upward curving, and also distinctly converging towards one another. Thus they come to lie very close under the pleural ridges, and pass forwards and upwards to a point very nearly vertically above the second coxæ, where they attain their maximum convergence, and are connected by the short stout thoracic anastomosis (TA) (a very short connecting trachea from which two small diverging branches pass to the region of the closed posterior stigmata). Beyond this, they diverge slightly, and pass close under, and a little to the inside of, the pair of larger and open anterior stigmata (St₁) which lie hidden in the fold between thorax and prothorax.

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Fig. 20.

_Austrolestes leda_ Selys, 9. Diagram of tracheal system of thorax in full-grown nymph, viewed from right side. The left visceral trunk (VT) crosses over to become hitched on to the right second pedal trachea (p₂), and a remnant (Vr) forms a small loop attached to the dorsal trunk (DT). The alar trunks (AT₁, AT₂) arise from DT (anally), and end (costally) on the second and third pedal trachea (p₂, p₃) respectively. The posterior stigma (St₂) is aborted, but its position is marked by tracheal branchlets. The two dorsal trunks (DT) are connected by a short transverse anastomosis (TA). For other letterings, see p. 214.

At a point not far removed from the thoracic anastomosis (slightly behind it in Enarsche, in front of it in Agrionidae), each dorsal trachea gives off a strong branch to the second leg, the second pedal trachea (p₂). This important trachea receives,
very close to its origin, the anterior termination of the visceral trunk from the opposite side of the body. That is to say, the two visceral trunks cross one another under the esophagus, the right one passing over the left, and each connects with the second pedal trunk of the opposite side. These visceral tracheae lie well below the dorsal tracheae, and play no part in the development of the wings.

At a point directly under the posterior part of the pleural ridge, not far from the point where the abdomen joins the thorax, each dorsal trunk gives off a short stout trachea, which enters the base of the corresponding hindwing-case at its anal end. This is the alar trunk of the hindwing. From it arise, in order, the anal, cubital, median, radial, subcostal, and costal tracheae of the wing-rudiment. This alar trunk is of greatest diameter at its point of origin from the dorsal trunk. As it proceeds costad, its diameter decreases. After giving off the six tracheae of the wing, it becomes a narrow, thread-like trachea. Its course through the wing-base is roughly semicircular. On leaving the wing, it runs downward and slightly forward, and finally enters the third pedal trachea \( (p_3) \), at a point very close to the posterior stigma \( (St) \). This third pedal trachea is itself an offshoot ventrally from the great dorsal trunk, and arises, in the \( Euchna \), not far from the alar trunk of the hindwing, which may be termed the second alar trunk. In the \( Agrionide \), owing to the greater obliquity of the thorax, it comes to lie very close under the origin of the first alar trunk.

The first alar trunk arises similarly to the second, from the main dorsal trunk. In the \( Euchna \), and probably in all \( Anisoptera \), this alar trunk lies very close to, and a little in front of, the second alar trunk. In the \( Agrionide \), it is separated from the latter by a greater space, and arises, as just mentioned, very nearly directly over the third pedal trachea \( (p_3) \). In the \( Anisoptera \), it is of somewhat smaller diameter analy than the second alar trunk; in the \( Zygoptera \), almost of the same size as the latter. It passes into the forewing-base at its anal end, gives off the six main wing-tracheae in the order already named for the second alar trunk, makes a semicircular loop, gradually decreases in diameter, and finally leaves the wing-base on its costal side as a fine thread-like trachea. It then runs downward and forward to join the second pedal trachea \( (p_2) \) somewhat below the point where the visceral trunk enters it.

In all \( Odonata \), the distance from the origin of the alar trunk to the point at which it gives off the anal wing-tracheae \( (A) \) is very short; while the distance from the point at which the costal wing-trachea \( (C) \) is given off, to the point where the alar trunk ends on the pedal trachea, is much longer, especially in \( Agrionide \). The diameter of each alar trunk is very much smaller at its ending on the pedal trachea than it is at its origin from the dorsal trunk.

It seems, therefore, very evident that the oxygen-supply of the developing wing in \( Odonata \) is derived from the anal end of the alar trunk, being drawn from the main dorsal trunk, which receives its supply from the branchial basket in \( Anisoptera \), or from the caudal gills in \( Zygoptera \). This fact is, in my opinion, the cause of all the chief peculiarities of the \( Odonate \) wing, as will be shown in Section B of this part.

The diagram in Fig. 20 shows a lateral view of the tracheation of the thorax in a larva of \( Austrolestes leda \) Selys, directly after the last larval ecdysis. The drawing was made under the camera-lucida by means of strong, artificial, transmitted light, in which all the tracheae appeared almost black on a pale yellowish-green ground. Making allowances for the greater obliquity of the thorax in the \( Zygoptera \), the results of my dissections of \( Euchna \) larvae agree very fairly closely with this diagram. I thought it advisable to publish the diagram of \( Austrolestes \) rather than of \( Euchna \), because the former can be much more easily studied, and the complete result verified; while, in the latter, only repeated dissections enable one to piece the whole scheme together, and thereby invite the unwitting introduction of error.

Section B.—General theory of the unique development of the \( Odonate \) wing-venation.

We are now in a position to enunciate a theory concerning the unique peculiarities of the wing-venation of \( Odonata \), in the following words.
The peculiarities shown by the wing-venation of Odonata, as contrasted with that of other insects, are due primarily to the aquatic habits of the larva; whereby, through the development of rectal or caudal breathing, the oxygen-supply of the developing wing is carried from the posterior end of the body, and enters the wing-base at its anal end.

The effects of the peculiar formation of the alar trunk may be stated as follows. (1) The costal trachea (C) is in the most unfavourable position for receiving oxygen. As a matter of fact, it receives scarcely any, dwindles rapidly in size, and becomes a mere rudiment in the fully developed nymphal wing.

(2) Next to C, the subcostal trachea (Sc) lies in the next most unfavourable position. It receives a certain amount of oxygen, but its development is weakened and curtailed, so that it only develops about half-way along the wing-rudiment. This fact, originally a source of weakness to the wing, has been seized upon by natural selection, and has been made a source of strength to the wing by the development of the unique formation known as the nodus at the end of Sc.

(3) The radius (R) was originally the largest and longest trachea of the wing (as may be seen by comparing the Odonate wing with that of an Ascalaphid, an insect undoubtedly derived from the same stock as Odonata, before the larvae of the latter adopted an aquatic mode of life). Originally R arose at the extreme bend of the alar trunk at some distance away from M, and thus held an excellent position for receiving the flow of gas from either costal or anal ends of AT. At first, it tends to develop ahead of the media (M), and at the ontogenetic period when both R and M appear as fair-sized bifurcated trachea, R is still greater than M.

(4) At this stage, M begins to gain on R, owing to its ability to intercept oxygen coming from the anal end of AT. Arising a little before the extreme bend of AT, M is in an exceptionally favourable position for competing with R for the flow of gas. As the wing develops, M begins to gain upon R, and finally moves up close to it, thus sharing with R the ideal position at the bend of AT, and receiving more oxygen than any other trachea in the wing. Thus it develops into a four-branched trachea supplying a greater area of wing-rudiment than is supplied by any other trachea.

It might here be accepted as sufficient explanation of the ultimate fusion of R and M in the imago, that it was the direct outcome of the struggle for precedence between these two leading tracheae of the wing. Certainly this played no inconsiderable part in the result. But there can be little doubt that another factor, viz., the gradual tendency towards the production of a narrower flying-wing from an originally broader planing-area, helped to drive these two tracheae close together. The same tendency also most certainly played a part in the invasion of territory originally served by R, by one or more branches of M. Partly because of this gradual wing-narrowing, partly also because of the gain in development by M at the expense of R, we find the former throwing two of its four branches over Rs, so as to invade and supply the area between R and Rs.

(5) The cubitus (Cu) was originally a much smaller trachea than either M or R. In a wing with a symmetrical oxygen-supply (i.e., a supply received equally from costal and anal ends of AT), Cu would develop about equally with Sc, its analogue on the costal side of the wing. But it lies in a more favourable position, in the Odonate wing, since it is closer to the anal oxygen-supply than any trachea except A itself. Hence it develops into a strong two-branched trachea of greater importance than any except R and M.

The weaker development of Cu (and A also) in the forewing is easily explained by the fact that the hind wing-case completely covers over this portion of the forewing. Thus, both Cu and A in the forewing are deprived of the light so necessary to the formation of strong pigmentation; and this must, in the end, have a deleterious effect on the development of this portion of the forewing.

(6) The anal trachea (A) is only a small trachea, which could develop but little, were it not for its extremely favourable position, enabling it to take first toll on the available oxygen-supply,
and thus to develop much more freely than its analogue (C) on the costal side of the wing. Hence, in the Odonate wing, it is enabled to become a four-branched trachea of considerable importance, particularly in the overlying hindwing. Also, it competes with Cu in the same manner that M competes with R; and hence arises the fusion of Cu and A already described in the imaginal wing. Of course, as in the case of R and M, the tendency towards narrowing also aids this result.

This theory, then, founded on the facts now known concerning the origin of the alar trunk, is sufficient to account for all the peculiarities of the Odonate wing, provided we accept also the theory, already advanced by Handlirsch, of the development of the present-day insect-wing from an original broad planing-area, only useful for accomplishing long downward "vols planés," and not for active flight. Probably nobody will now refuse explanation and lirsch's theory, since it appears to be the only possible explanation of the development of any form of wing in Nature. It is not, however, the object of this Section to discuss Handlirsch's theory. We may safely claim it as a contributory cause to the peculiar development of the Odonate wing-venation, while, at the same time, indicating the anal oxygen-supply as the primary cause of all those peculiarities.

Let us now go back a little further, and inquire what evidence there is, either in Ontogeny or Palaeontology, for the belief that the larva of Odonata were not originally but only secondarily aquatic in their mode of life. The evidence for this seems to me to be overwhelming, but there are some important points that bear more closely on the question at issue.

First of all, if the Odonata larva took to fresh water from the sea, without the intervention of a land-living period, we should naturally expect to find them still breathing by those archaic adaptations of segmental processes which, we have every reason to believe, were employed by Trilobites and their nearest allies. The fact that the larvae of both Anisoptera and Zygoptera exhibit breathing-organs utterly unlike those of any other aquatic animal, speaks very strongly in favour of a special development of these organs in larvae which, having lost their original marine mode of respiration by taking to the land, again took to the water and developed organs peculiar to themselves.

Secondly, the persistence of thoracic spiracles, in spite of their uselessness during the greater period of growth, is a strong argument for the existence of an open tracheal system in the larvae as well as the imagines of the ancestors of our present-day Odonata.

Thirdly, a careful study of the peculiar connections of the leg- and wing-tracheae in the larvae of Odonata must go far to convince us of the same truth. Let us examine these in detail.

The anterior spiracle (St₁) in the larva is still open, and partly functional. Now p₂ arises from St₁, and a branch lb passes off from it to supply the labium. On the other hand, p₁ arises directly from DT, and receives only a small branch from St₁.* This can be understood, if we suppose that this small branch was the original p₁, and that, later on, a new attachment was developed on to DT, to intercept the oxygen coming from the anal end of the body.

Again, p₂ arises directly from DT, but it gives off one or more small tracheae to the region of the closed posterior stigma (St₂). The same explanation would, therefore, hold here, viz., that these small branches represent the remains of the original trunk of p₂ (now almost aborted by the complete closing of the stigma), while a new attachment was formed on the dorsal trunk (DT) when the larva took to breathing from its anal end.

Let us now see whether the other tracheae of the thorax support this explanation.

Firstly, the visceral longitudinal tracheae (VT) cross one another in a peculiar manner, and terminate each on p₁ of the opposite side, not far below the stigma. This is an extraordinary arrange-

* This is the arrangement in the Anisoptera. In the Zygoptera, p₁ arises from DT in front of St₁, while p₂ connects up to St₁ (Fig. 201. Either of these arrangements is clearly of a secondary nature.
ment. It can scarcely be doubted that these visceral trunks were originally developed from St1 for direct air-breathing, and that the present crossing and hitching on to p3 is a secondary arrangement developed when the larva took to an aquatic mode of life.

Secondly, the alar trunks, by their peculiar arrangement, support the theory of an original air-breathing larva for Odonata. Each ends by a slender attachment to its corresponding pedal trachea (p4 or p5) not very far from the stigma. These slender endings are at present of no value to the developing wing, since it is quite clear, from the gradual decrease in diameter, that the oxygen supply now comes altogether from the anal end. What then can they be, but the reduced remnants of the original alar trunks, which arose either directly from the spiracles, or, more probably, from the pedal tracheae close up to the spiracles? In that case, there must have been originally, in the air-breathing larva, a supply of oxygen to the costal side of the wing-base, such as is found in the larvae of all present-day insects except the Odonata. Whether this supply arose directly from the stigma or from the pedal trachea, or even originally from the main visceral or ventral trunk, it is scarcely necessary to enquire. The point is that the Protodonate wing was developed along normal lines, by means of an oxygen-supply to the costal side of the wing (probably also, as in Plecoptera, with a smaller supply to the anal side), and that this normal method of supply was destroyed when the larva took to fresh water. From that point onwards, we must expect to see the gradual development of those peculiar characteristics which make the Odonate wing unique.

One more point of interest in this question can be brought forward. It is well known that the whole dorsal tracheal system in Odonata is of a peculiar reddish-purple or bright coppery colour, while the visceral system is silvery-white. Now, just where the main dorsal trunk passes close to the anterior stigma (St1) it divides into two parallel, main trunks supplying the head (Fig. 20). The outer of these seems to represent the original dorsal trunk, while the inner probably represents an originally separate tracheal system for the head, which became hitched on to the dorsal trunk when its original air-supply was cut off by the more or less complete functional atrophy of St1. (The short branch to St2 is still to be seen). Now (Fig 20) whereas all these tracheae are either purplish-red or coppery colour, and hence belong to the dorsal system, there can be easily detected, lying just inside DT, a very short trachea (Vr) of silvery-white colour, arising from the inner of the two divisions of DT close to the point where it divides into two, and running back only a very short way to enter again the dorsal trunk itself. What then can this useless rudiment be, but the original spiracular ending of VT, the rest of which is now broken off and hitched on to p3? Surely its silvery colour admits of no other interpretation, since at the present time it is completely attached to the dark coloured dorsal system!

Let us now turn to Paleontology for support. If our theory be correct, the ancestors of our Odonata should show a stronger development of the tracheae on the costal side of the wing than they do to-day. Also, no water-dwelling larve should be found in those deposits whence we have obtained such ancestors. Now this is exactly the case with our Protodonata. Fossil Ephemerid larvae are recorded far back, almost into Palaeozoic times; but no fossil larvae referable to an Odonate type have yet been found with them. Moreover, in the Protodonata, Sc runs either to the wing-tip or nearly as far, while the crossing of one or more branches of M over R is not accomplished, nor are M and R fused in the imago. Further than this, the Protodonata exhibit extraordinary differences, in many cases, between the venation of fore and hindwings—differences that seem to defy explanation, unless we assume that these insects are misnamed, and do not lie anywhere near the direct line of Odonate ancestry. Might not an application of this new theory help to solve some of these very difficult problems, on the assumption that the tracheal shiftings took place not only gradually but also unequally in fore

*The remarks in this paragraph apply, as regards colouration, specially to the Anisoptera. In the Zygoptera, the arrangement of the trachea is similar, but the differences of colouration are not so marked.
and hindwings, thus producing differences in the venation? Such an application, though beyond the scope of the present paper, would be well worth making by some student more intimate with the vagaries of Protodonata wing-venation than myself.

There remains now to be carried out a thorough study of the embryonic and early post-embryonic development of the tracheal system in Odonata. Such a study will almost certainly reveal the true phylogenetic stages of Odonate larval history, and I hope to be able to give a full account of them in a future paper. If it should be proved to bear out the theory offered in this Section, we shall have, in the Odonata, a double tracheal metamorphosis—first from spiracular to anal breathing in the young larva, and secondly from anal breathing back to spiracular breathing at metamorphosis—which will be more wonderful even than the remarkable changes, now known to every biologist, which took place in the blood-system of the Vertebrata when they began to desert the sea and make their homes on dry land—changes which to-day are being repeated in the ontogeny of every air-breathing Vertebrate.

REFERENCE LETTERS.

A, anal trachea or vein: A₁, A₂, A₃, A₄, its four branches—A' secondary anal vein—Ab, anal bridge—Ae, anal crossing (="first cubito-anal cross-vein")—Al, anal loop—A₁', secondary anal loop (of Euchna)—arc, arcuinus—At, anal triangle—AT₁, AT₂,alar trunks of fore and hindwings—B, bridge-vein—C, costal trachea or vein—Cu₁, Cu₂, its two branches; Cu₃a, Cu₃b, distal and proximal branches of the latter—Cul, cubito-anal or Italian loop—Cuspl, cubital supplement ("midrib of Italian loop")—DT, dorsal longitudinal tracheal trunk—Fw, forewing—Hd, head—Hw, hindwing—lr, labial trachea—M, median trachea or vein—M₁, M₃, M₄, its four branches—mm, membranue—MM, combined meso- and metathorax—Mspl, median supplement—N, nodus—o, oblique vein—P₁, P₂, P₃, first, second and third pedal trachea—Pr, pleural ridge—Pt, prothorax—ps, branch-trachea to region of second stigma—R, radial trachea or vein—R₁, R₂, its two branches[Rs="radial sector"]—Rspl, radial supplement—Sc, subcostal trachea or vein—sl, subtriangle—St₁, St₂, anterior and posterior stigmata, or spiracles—t₁, triangle—TA, thoracic or posterior tracheal anastomosis—Vr, remnant of visceral trunk—VT, visceral longitudinal tracheal trunk.
DEVELOPMENT OF THE WING-VENATION OF ODONATA.

Fig. 4. — *Austrolestes cingulatus* Burm.,♂. Corresponding venation in imago.

Fig. 5. — *Syngastes wuyersi* Selys,♀. Tracheation of forewing of nearly full-grown nymph. (Compare Plate xiii., fig. 2).

Fig. 6. — *Syngastes wuyersi* Selys,♂. Corresponding venation in imago.

Fig. 7. — *Argiolestes griseus* Selys,♀. Tracheation of forewing of full-grown nymph. (Compare Plate xiii., fig. 3).

Fig. 8. — *Argiolestes griseus* Selys,♂. Corresponding venation in imago.

Fig. 9. — *Neosticta canescens* Tillyard,♀. Tracheation and imaginal venation of forewing of full-grown nymph. (Compare Plate xiii., fig. 4).

Fig. 10. — *Neosticta canescens* Tillyard,♂. Corresponding venation in imago.

Fig. 11. — *Isosticta simplex* Martin,♂. Tracheation of hindwing of nearly full-grown nymph.

Fig. 12. — *Isosticta simplex* Martin,♀. Corresponding venation in imago.

(All figures of nymphal tracheation from microphotographs; x 30. Figures of imaginal venation from camera-lucida drawings; x 5).

Plate xiii. (Microphotographs).

Fig. 1. — *Caligarion billinghursti* Martin,♀. Tracheation of hindwing of full-grown nymph. (Compare Plate xii., fig. 1).

Fig. 2. — *Syngastes wuyersi* Selys,♀. Tracheation of forewing of nearly full-grown nymph. (Compare Plate xii., fig. 5).

Fig. 3. — *Argiolestes griseus* Selys,♀. Tracheation of forewing of full-grown nymph. (Compare Plate xii., fig. 7).

Fig. 4. — *Neosticta canescens* Tillyard,♀. Tracheation of forewing of full-grown nymph. (Compare Plate xii., fig. 9).

(All figures x 50.)

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Wing-venation of Odonata.
Wing-venation of Okinada.