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## The Evolution of the Order Odonata.

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### (Abstract.)

Many years of study of the Order Odonata has convinced me that the larval wing-tracheation, while corresponding in general with the imaginal venation, cannot be relied upon to determine the veins in every detail. In particular is this the case with the vein which Needham originally called Rs and which I later on termed Ms. In the Anisoptera, the trachea of this vein crosses over two branches of the vein which Needham terms the media, M. In Zygoptera, it is always supplied by a branch trachea from this vein M, without any crossing over. But the origin of this trachea differs in different groups; in *Lestidae* the trachea starts far distad, leaving a long basal portion of the vein, called the "long bridge", destitute of a trachea: in most Zygoptera the trachea comes off from M at the same point as the vein, so that there is no bridge at all: and in some larvae of *Synlestes*, the trachea actually arises from the branch of M posterior to Ms.

The fact that there are four different sources of supply for the trachea of vein Rs or Ms strongly suggested to me that it was the tracheation that was variable, not the vein. When the Upper and Lower Permian Odonata were discovered, they all turned out to be exceedingly primitive Zygopterous forms allied to *Hemiphlebia* and *Chorismagrion* of Australia to-day, with the discoidal cell open basally and a very primitive type of nodus and arculus. I therefore studied the condition of the so-called Rs or Ms in these types, and discovered at once that it was not a true primitive vein, but an interpolated vein of the same type as  $M_{IA}$  of Needham, with a Y-vein connection to the two veins anterior and posterior to it. As  $M_{IA}$  has no trachea, I argued that, in the most primitive larval form, Rs or Ms should not have a trachea either. Last year I revisited Australia and was enabled to make an expedition to the original locality where I discovered *Hemiphlebia mirabilis* Selys more than twenty years ago, and took over fifty larvae of it there. Dissections of these show that the so-called Rs or Ms has no trachea in that larva, nor has  $M_{IA}$ , nor has the vein called  $M_4$  by Needham, nor the vein  $I_A$ . In fact, only R and the concave veins possess tracheae.

If this is an indication of the primitive type of venation, it is too far back for the fossil record at present. But we have to note that all the Megaseoptera and Palaeodictyoptera have Rs with only concave branches, and that, in the Protodonata, Odonata and Plecoptera, convex veins are interpolated between them. It therefore follows that the ancestral Order from which these three more specialized Orders have been derived must have a

radical sector of this type. In looking for the ancestor of the Odonata, we have to find something close to the Permian types, i. e. with only a single anal vein and also a petiolate or subpetiolate base. Another character which may give us valuable guidance is that the wing is hairless and the costa is strongly serrated along its outer edge.

The Megasecoptera being the only Order with a single anal vein, and many of the forms having petiolate or subpetiolate wings, I conclude that they must be the ancestral Order. Further, the Carboniferous genus *Brodiea* has the strongly serrated costa, and also a small humeral hump suggestive of the beginnings of a precostal area such as is found in Protodonata. The venation of the last larval instar of *Brodiea* is known as well as that of the imago; between the two lies a hypothetical type which I call *Protobrodiea*, having only two descending concave branches of Rs, which is exactly the type needed for us to develop evolutionarily the whole series of Protodonata and Odonata. The Protodonata are a side-branch, starting with *Campyloptera* in the Upper Carboniferous and having two families, the *Protagriidae* (*Protagrion*, *Calvestiella*) with the true Rs still distinct and the *Megansuridae* (*Megansura*, *Megatypus*, *Typus*, etc.) with Rs and MA fused and MP and  $Cu_1$  already reduced. The stages of evolution of true Odonata are a hypothetical *Protokennedya* in the Carboniferous, from which the Protodonata branched off as a high specialization, followed by the actual fossil form *Kennedya* itself in the Lower Permian, then by the slightly more specialized *Permagrion* and allied unnamed forms in the Upper Permian. These latter are the first true Zygoptera, and they all have petiolate wings, two antenodals, and an open discoidal cell.

Living remnants of this group are the genera *Chorismagrion* and *Hemiphlebia* of Australia. The next stage is the closure of the discoidal cell to form a complete quadrilateral, with completion also of the subnodus, and recession of the branches of Rs basad. Following on that line comes a whole succession of Zygopterous forms in which the general tendency is for fore and hind wings to remain similar, but the anal area to grow and to eliminate the petiolation. It is therefore logical to group the Suborder into the two main divisions or superfamilies of *Coenagriioidea*, retaining the primitive condition of two antenodals, and *Agrioidea*, with more than the original two, provided we remember that there are some annectant types still in existence between them. The culmination of the Zygopterous line lies in the brilliant *Agridae* or *Calopterygidae* of De Selys.

Far back in the Trias, in a group of genera not far removed from *Hemiphlebia*, a tendency set in for the hind wing to develop ahead of the fore. The first differentiation was that the quadrilateral of the hind wing became closed basally, while that of the fore remained open. Next the forewing quadrilateral tended to narrow and bend transversely to the wing, while the hindwing quadrilateral widened as the wing widened. The Triassic and Liassic forms which show this tendency more and more developed as placed in the intermediate Suborder Anisozygoptera, of which only the genus *Epiophlebia* is living at the present day. No true Anisoptera can be proved to have lived in the Liassic, but the Upper Liassic genus *Gomphites*, represented by a hindwing only, is very close to the existing Petalurid genus *Tachopteryx*. Probably it still had a simple quadrilateral

in the forewing, and was therefore not *Tachopteryx* itself, but its immediate ancestor.

There can be no doubt that the true Anisoptera are derived from the Anisozygoptera of the *Gomphites* type, and that they first appeared in the Jurassic, being represented then by a large number of Petalurid and Gomphid types. As a side-branch from the *Petaluridae*, the *Petalia*-group developed, and the uncoloured extinct forms of this group gave origin to the *Aeschnidae*. Another side-branch from the *Petaluridae* was ancestral to the *Cordulegasteridae*, and those forms in which differentiation between fore and hind wing quadrilaterals was most highly developed evolved into the *Corduliidae* with the *Libellulidae* as a specialized sidebranch. This latter has by now become the most highly successful evolutionary effort of the whole Order.