

SOME ARMCHAIR THOUGHTS ON THE DRAGONFLY WING

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An introductory guide to modern dragonfly wing venation is presented. Some remarks are made on tracheation, and on the venational nomenclature of the theory of pre-tracheation. The wings of fossil dragonflies are then considered. The meganeurids, the Protozoptera, the Protanisoptera, the Liassic Anisozoptera, and the Jurassic and Tertiary fossils are discussed in turn. Finally the primitive and specialized features of venation are considered.

INTRODUCTION

Much of the classification of the Odonata is based on wing venation. This makes for a clear and soundly based taxonomy, enjoyed by few other insect groups. But often to the beginner venation seems tiresome and obscure, as there is a fair number of special terms to be mastered, and the subject is frequently poorly presented. Often in articles on Odonata a particular venational feature is termed 'primitive' or 'modern', or allusion is made to some fossil wing of which the unfortunate reader has never seen a picture, leaving him confused. Which venational features are primitive, and which specialized, and what sort of evidence exists for calling them so?

After finding myself baffled several times in the course of my reading, I decided to spend odd moments of spare time in the university library, while still lucky enough to have access to one, and to look up some of the articles on fossil wings, to see the evidence for myself. Having now satisfied my own curiosity, it has occurred to me that setting down some ideas on paper might save other beginners time and trouble.

The simple comments below are freely borrowed, and unoriginal. I am no palaeontologist, and in no way claim to offer a complete survey. There are already authoritative articles on the classification of the Odonata. All that I am

aiming at it to provide a beginner's guide to the subject of venation, in a palatable form.

MODERN VENATION

Before embarking upon the discussion of fossil dragonfly wings, it is necessary to make some remarks about the naming of veins. Unfamiliarity with these terms and their contractions can make the simplest points appear obscure.

Let us take out from our storebox two dragonflies, a coenagrionid zygopteran and an aeshnid to represent the Anisoptera. At this stage, the names may serve simply as labels. The nomenclature followed is essentially that of Tillyard, in his later work, which is the system used by most British odonatologists.

We will start with the simpler coenagrionid venation. The forewing and hindwing are alike in shape, and slender at the base, for which the usual term is 'petiolate'. Counting from the front, there are five main veins, named the costa (C), the subcosta (Sc), the radius (R), the media (MA), the cubitus (CuP), and the anal vein (IA). The hind margin of the wing has no special name. R and M are fused basally, and so appear as only one vein to the naked eye.

The costa runs as the full anterior margin of the wing, jointed a third of the way along at the strengthened nodus. The subcosta runs only as far as the nodus. The radius goes straight out to the wingtip. Between it and the costa are the antenodal cross veins (Ax), two only, which cross the subcosta, and several postnodals (Px). The coloured cell at the apex between C and R is the pterostigma, or stigma for short.

Below R+M is the most complex part of the venation, the arculus and quadrilateral. The arculus (Arc) is the little crossvein joining R+M to CuP. Two veins run out distally from it. The upper is a branch of R, the radial sector (RS), and the lower is the media. The latter is an unbranched

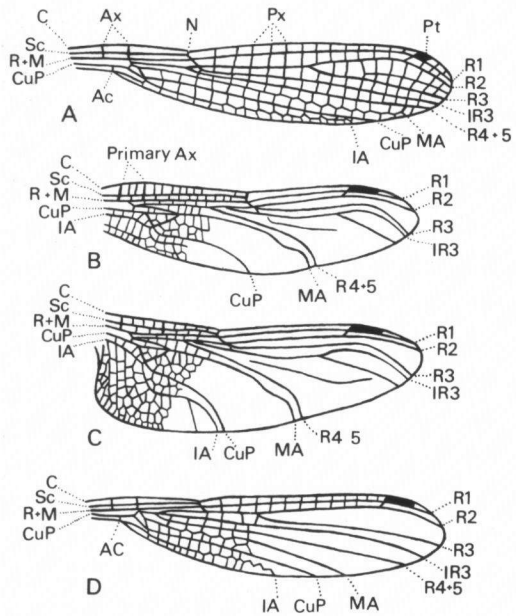


Fig. 1. Examples of modern venation: (A) coenagrionid, *Pseudagrion* Fw; - (B) aeshnid, *Aeshna* Fw; - (C) the same, Hw; - (D) lestid, *Lestes* Fw.

vein, but RS divides up distally. The first branch turning down is R4+5, and the continuation of RS is now termed R2+3. R2+3 divides as its name suggests into R2 and R3, R3 being the lower branch. R4+5 usually remains undivided, and in this case is more simply thought of as R4. Into the fork between R2+3 and R4+5 fits the intercalated vein IR3, and into the fork between R2 and R3 fits the similar IR2.

CuP comes out from the base, then along the bottom edge of the quadrilateral, and finally out to the wing margin. IA appears to start, not from the base at all, but from the hind margin of the wing a little way along. However in some coenagrionids it can be seen to start from the base, and run fused with the wing margin for a short distance before leaving it. A small crossvein hitches IA up to the outer corner of the quadrilateral before it proceeds distally. At the start of the free anal vein from the hind margin, there is a small stout crossvein reaching up to CuP. This is the anal crossing (Ac).

We are now in a position to state which are the veins forming the quadrilateral, alternatively termed the discoidal cell. Its upper and lower borders are segments of MA and CuP respectively. Its inner border is the lower half of the arculus, and its outer border a simple crossvein.

Let us now turn our attention to the aeshnid wing. Here the wings are dissimilar in shape, but the general plan of the five main veins is the same as in the coenagrionid wing. However, a few differences must be noted. There are many Ax instead of two, although two are stouter than the others (primary Ax). Below the strengthened veins of the nodus, between R3 and IR3, is a little crossvein which is stouter than its fellows, the oblique vein (o). At the base there is an evident triangle of veins. Comparing this structure with the simpler coenagrionid quadrilateral, it is clear that essentially two modifications are needed to develop the triangle. Firstly the lower half of the arculus has moved basally, away from the downcurve of CuP, and the downcurve itself has become sharper. Secondly a 'roofing strut' has been added, reaching across

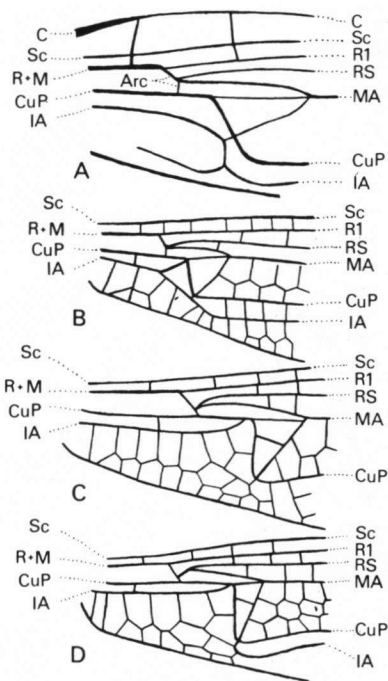


Fig. 2. The anisopteran triangle: (A) aeshnid, *Aeshna* Fw; - (B) gomphid, *Gomphus* Fw; - (C) corduliid, *Cordulia* Fw; - (D) libellulid, *Sympetrum* Fw.

from the bend in CuP to close the triangle.

The anal vein of the aeshnid has quite unequivocally a separate origin from the base, but Ac is still present. IA is quite firmly bound to the lower corner of the triangle, before continuing on, branching distally in the hindwing, which accounts for the broadness of the hindwing compared to the forewing. Additional looped veins below IR3 and MA respectively are the radial and medial supplements (Rspl and Mspl).

This is not the place to attempt a thorough discussion of the different venations within the modern Odonata, but it is as well to mention the main types which exist.

In the coenagrionids, R4+5 originates near the subnodus, and the start of IR3 is also attached there. The stigma is a parallelogram, the quadrilateral a trapezium, and IA is long. In the lestids R4+5 originates well proximal to the nodus, and the

Table I
Notation for main veins

Vein	TILLYARD (1926)	FRASER (1949)	NEEDHAM (1951)	Selysian
<i>Costa</i>	C	C	C	Costal nervure
<i>Subcosta</i>	Sc	Sc	Sc	Subcostal nervure
<i>Radius + Media</i>	R1+Rs	R+M	R+M	
<i>Radius</i>	R1	Ri	R	Median nervure
<i>Branches of radial sector</i>	R2	Rii	M1	Principal sector
	R3	Riii	M2	Nodal sector
	R4+5	Riv+v	M3	Median sector
<i>Radial sector</i>	Rs	RS	M1+3	Upper sector of arculus
<i>Intercalated vein</i>	IR3	IRiii	Rs	Subnodal sector
<i>Media</i>	MA	MA	M4	Lower sector of arculus, then short sector
<i>Cubitus</i>	Cu2	CuP	Cu1	Upper sector of triangle
<i>Analís</i>	IA	IA	Cu2	Lower sector of triangle
<i>Arculus</i>	arc	Arc	ar	Arculus
<i>Anal crossing</i>	Ac	Ac	Ac	Submedian nervule

The old Selysian notation quoted above is that given by RIS (1909). NEEDHAM (1951) offered a table comparing the Selysian names with his own system, and recommended the retention of the terms 'Upper and Lower sectors of the arculus' for the radial sector and the initial part of the media after the arculus. LONGFIELD (1960) gave a fuller table, including Tillyard's earlier notation, based on Needham's, and Ris' notation, also based on Needham's but using the term Cuq for Ac. Longfield preferred the name Cu2 to Fraser's CuP for the posterior cubitus.

start of IR3 has also progressed basally. The stigma is long and approximately rectangular, while at the quadrilateral the downcurve in CuP is sharp. In the protoneurids the quadrilateral is rectangular, and IA may be short, sometimes only a cell or two long.

These groups have simple venation readily comparable to the basic coenagrionid type, but in the calopterygid wing dissimilarities occur. The venation is denser, with many antenodals and altogether more cells. R4+5 and IR3 start proximal to the nodus. The quadrilateral is rectangular, and very long, with its distal edge strengthened and prolonged downwards to meet IA. IA has a clearly separate origin from the base, as in Anisoptera.

Among the Anisoptera the chief variation in venation occurs at the triangle. In the aeshnids the triangle is elongated sideways, sometimes markedly so, and it is the only triangular structure. In the gomphids the triangle approaches the equilateral. As it bends down to touch the lower corner of the triangle, IA throws off a stout crossvein to the upper proximal corner of the triangle, and a subtriangle is thus formed. In the libellulid forewing, this process has gone further. IA follows the crossvein into the upper corner of the triangle, and its original bend down to the lower corner is lost. But one picks it up again running distally from the lower corner as before. The forewing triangle is elongated anteroposteriorly. The hindwing retains the gomphid arrangement, so that triangles in forewing and hindwing are dissimilar.

The aeshnids and gomphids retain two hypertrophied antenodals, whereas the corduliids and libellulids show no sign of them. The corduliid nodus is relatively distal in position.

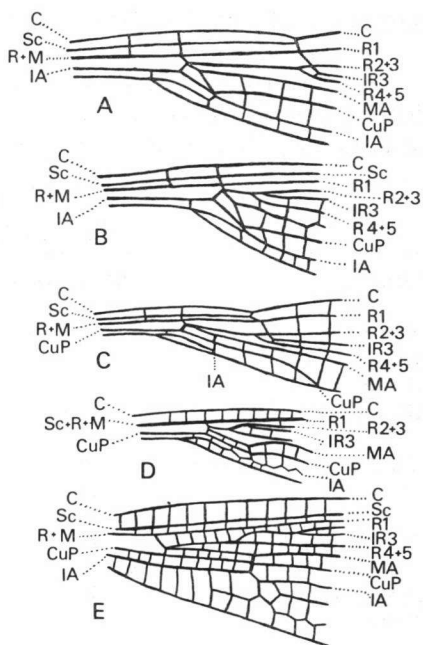


Fig. 3. The zygopteran quadrilateral: (A) coenagrionid, *Pseudagrion* Fw; — (B) lestid, *Lestes* Fw; — (C) protoneurid, *Elatoneura* Fw; — (D) calopterygid, *Chlorocypha* Fw; — (E) calopterygid, *Phaon* Fw.

FOSSIL DRAGONFLIES: GENERAL REMARKS

Insect fossil records of any consequence begin in the Upper Carboniferous,

some 250 million years ago. Several evolutionary lines were already present at this time, dating the origin of winged insects still further back.

Most of the Carboniferous insects were palaeopterous, with their wings moving only up and down, and not folding back along the body, and only a minority neopterous, with wings folding down over the back. Today the vast majority of insects are neopterous. The palaeopterous orders of the Carboniferous were five. Three of them comprised mayfly-like insects, the Palaeodictyoptera, Protoephemeridae, and Megasecoptera. The other two orders were the Protohemiptera and the Protodonata. The neopterous insects were the forerunners of locusts, cockroaches, and stoneflies. Of the old palaeopterous groups, only the Protodonata survived the Permian age.

By the Jurassic the Protodonata had become extinct. The earliest Diptera and Hymenoptera are found in Jurassic strata. The Cretaceous insect fauna is virtually unknown, which is regrettable since rapid development took place during this period, presumably to some extent in step with the evolution of flowering plants. By the early Tertiary the insect fauna is extremely modern in type. A good source of evidence is the Baltic amber, formed from pine resins 50 million years ago. From amber several extant genera and even species have been identified.

To see the antiquity of the dragonflies in perspective, it may be mentioned that by the Jurassic they were relatively modern in form, yet it is from contemporary deposits that the earliest known fossil bird, *Archaeopteryx*, comes.

In a lively account of fossil dragonflies, CORBET (1960) has drawn attention to some of the chief points of interest about their evolution. What did the early dragonflies eat before the evolution of the Diptera, their main food today? At what stage did their nymphs become aquatic? When and how did their almost unique method of copulation evolve? These fascinating questions are not our concern here.

We will now go on to deal in more detail with the evolution of the dragonfly wing. The fauna of the Upper Carboniferous is of interest in two respects, firstly for the light shed on the origins of dragonfly wing venation, and secondly for the specific dragonfly fossils it provides.

Let us take the first question first. TILLYARD (1938) gave a clear account of the subject, but it is as well to mention the salient points. Several workers have made the assumption that the archetypal insect wing venation approximated to that of the Palaeodictyoptera, for the reasons that these fossils had an evidently unspecialized venation, and are among the oldest fossils known. This assumption is open to dispute, but let us take it as a working hypothesis and see where it leads.

The Palaeodictyoptera have five main veins originating at the base of the wing, costa, radius, media, cubitus, and analis. The belief that dragonfly venation is derived from a palaeodictyopteran-like ancestor determines the use of the

same terminology for the veins. These main veins branch as they run apically. In 1922 LAMEERE formulated the hypothesis that in the archetypal venation each main vein divided into an anterior convex and a posterior concave branch, for which he employed the term "sector". These principal branches then divided further distally. Such a fluted arrangement is presumed to give strength combined with flexibility to the wing. This postulated arrangement holds good for the Palaeodictyoptera, with the exception that no sector of the analis has been certainly identified. The branches of the main veins are named as follows: costa divides into costa and subcosta, radius into radius and radial sector, media into anterior and posterior media, cubitus into anterior and posterior cubitus, and analis as we have said, not at all.

Casting back to the coenagrionid venation discussed earlier, the costa, subcosta, radius, radial sector, and analis are all recognizable. There remain only two veins, whereas according to the theory there ought to be four. Therefore the dragonflies have lost two veins, one convex and one concave. This is true of the earliest dragonfly fossils.

In a long article on the venation of dragonflies and mayflies, MARTYNOV wrote in 1930: "As I approached the study of the venation of dragonflies and mayflies I thought that if the dragonflies and ephemerids were Palaeoptera, then not only the mayflies but also the dragonflies should preserve the features of venation of the related Palaeodictyoptera." The conclusion that he arrived at is that the two veins remaining in the centre of the dragonfly wing between RS and IA should be designated M, without being certain whether it is MA or MP, and CuP, implying that the anterior cubitus has been lost. If we wish to conform to the theory of alternating concave and convex veins, then the vein M must be designated MA, as it is convex, and this is the term which has gained general acceptance. In modern Odonata Sc, RS, and CuP are concave, while R1, IR3, MA, and IA are convex.

If one accepts the notation of NEEDHAM (1951) with the radius crossing the media, which we will discuss below, then dragonfly venation must stand in an isolated position, and attempts to homologize venation among the palaeopterous orders become untenable. Martynov and many other workers prefer to assume that homologies do exist, and attempt to argue back from them to arrive at the correct names for the veins.

TRACHEATION

At some juncture a few words are needed on tracheation. The most casual student of the Odonata will run up against the fact that different systems of nomenclature exist for the veins. Pre-eminent among these are two, that of Tillyard in his later work, which is the one which we are employing here, and that of COMSTOCK & NEEDHAM (1898), which is usually described as being

based on tracheation.

In the dragonfly nymph the veins develop in a jelly-like material contained within the sheath of the wing bud. The developing wing is supplied with oxygen by tracheae, which spring from a main trunk on each side, ultimately coming from the respiratory surface. The tracheae supply the developing veins. It is not clear to what extent the veins need more oxygen than the surrounding jelly. Thus we cannot be sure whether the tracheae follow the veins because the latter are greedy of oxygen, or because they simply form convenient struts on which to hang. Be that as it may, the tracheae do in general follow the veins.

The tracheation of the Anisoptera is altogether more extensive than that of the Zygoptera. The most extreme reduction of the tracheal system is found in *Hemiphlebia*. Whereas in the anisopteran wing all the major veins have their own tracheae, in *Hemiphlebia* IR2, IR3, MA, and IA have no special tracheae, getting their oxygen supply from small bifurcating branches of neighbouring tracheae. Even in Anisoptera the veins near the front edge of the wing do without strong tracheae, the costal tracheae being very short.

The Needham doctrine of pre-tracheation assumes that the course of the tracheae is the fundamental fact, and that the veins follow the tracheae and ought to be named accordingly. The contrary view holds that the veins decide their own course, and the tracheae adapt themselves to the vagaries of vein evolution as best they can.

The first place where detailed discussion is necessary is the tracheal supply of IR3. In the Anisoptera the trachea for IR3 springs from that of R1, passing down the subnodus, briefly along R3, and then down the oblique vein to IR3. This is why Needham speaks of the radius 'crossing over', because the trachea for

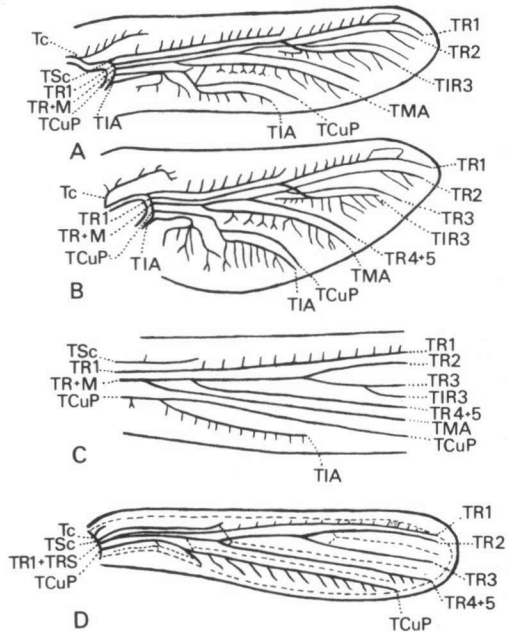


Fig. 4. Examples of tracheation: (A) anisopteran Fw; — (B) the same, Hw (both after NEEDHAM, 1903); — (C) zygopteran (after TILLYARD, 1914); — (D) *Hemiphlebia* (after FRASER, 1957). The position of the veins is shown by dotted lines.

IR3 does cross over. In his notation RS is written as M1+3, and the branches of RS become M1, 2, and 3. IR3 is written as Rs, MA as M4, CuP as Cu1, and IA as Cu2. Thus in his notation, the radius crosses over the media. The opposite view is that IR3 is a secondary intercalated vein, which in the course of evolution grew in strength, pushing back towards the base and, requiring extra oxygen, happened to borrow a branch of the trachea of R1.

In the Zygoptera IR3 gets its tracheal supply without any crossing over. In the coenagrionid wing the trachea for IR3 comes off that of RS at the nodus. In the lestid it comes off the R3 trachea beyond the nodus, leaving the basal part of IR3, termed the bridge, unsupplied. In the calopterygid it arises near the origin of IR3 basally. In all these cases, the descent of the trachea to IR3 is marked by an oblique crossvein.

Needham explains the failure of the trachea for IR3 to cross over in the Zygoptera by saying that they have secondarily lost the crossing. In other words the trachea for IR3 has separated from its previous origin at R1, and become attached to the trachea of RS or a branch of RS, the exact site varying in the different groups. The argument presupposes that the anisopteran venation is ancestral to the zygopteran.

The next place of particular note is the tracheation of IA. In many Zygoptera, as we have seen, the free IA commences at the hind margin of the wing, and not at the base. The IA trachea is not always readily made out in zygopteran nymphs, but when it is to be seen, it runs first along CuP, and then descends, by way of Ac, the anal crossing, to its destination. This inward loop of the trachea is evidently related to evolutionary reduction of the base of the wing, during petiolation.

In the Anisoptera, in which the anal vein arises separately from the base of the wing, the trachea still makes the same deviation, that is, it turns up to run along with the trachea of CuP, and then down Ac to IA. In an early discussion of this fact, when he was inclined towards the theory of pre-tracheation, Tillyard wrote that since IA by definition followed its trachea, it was to be considered as running with CuP, invisibly fused with it, and then down as Ac, and out laterally. The basal part of the anal vein was to be thought of as a secondary backgrowth, and not part of IA proper.

Fraser has however pointed out that in some Zygoptera, most notably the Australian *Hemiphlebia*, previously considered to have no trace of the basal portion of IA, a basal portion may sometimes be discovered, at times quite free, at times fused with the hind margin in a doubled-barrelled manner. If one regards *Hemiphlebia* as a primitive insect, there is no justification for thinking the basal part of IA a secondary backgrowth, if it possesses one. In other words, during reduction of the base of the wing, the trachea of IA may well have been driven inwards to lie close to the trachea of CuP, but the basal part of IA was not driven in to the same extent. It either came to lie very close to the hind

margin, sometimes actually fused with it, or disappeared altogether.

Ac is remarkably constant in its presence in the Odonata. FRASER (1954) wrote that the phylogenetic importance of this short cross nervure Ac cannot be exaggerated. Its continued presence in the Anisoptera, in which IA does originate from the base of the wing, when simplicity alone would predict that the IA trachea would run straight out along IA, rather than taking a circuitous course via CuP and Ac, is one of the best pieces of evidence for the origin of the anisopteran wing from a wing with a petiolate stalk.

The IA trachea which we have been discussing is always short, and only reaches as far as the bottom corner of the discoidal cell. The distal part of IA obtains its tracheal supply from the trachea of CuP. The theory of pre-tracheation leads to the nomenclature of Cu1 and Cu2 for CuP and the distal part of IA respectively. Curiously, in the oldest zygopteran fossils, the Protozygoptera, IA arises neither from the hind margin nor from the base, but from CuP. One might retain the suspicion that the distal, post discoidal cell, part of IA belongs in fact to the cubitus. However, CuP is concave and IA convex. We will continue here to use the term IA.

At this juncture we will leave the subject of tracheation. If the reader is unsatisfied with such a brief treatment, he may read more about it elsewhere. Some of the writings on the topic, notably those by Needham and Fraser, make lively reading, being somewhat acrimonious. It may be felt that the whole business makes too much of a fuss about notation. Does it matter what a vein is called, as long as it is plain what is meant? But the reader will have realized that discussion of tracheation at once involves the whole question of the status of the anisopteran wing. Did it give rise to the petiolate zygopteran wing, or did it instead develop from it? This is an absolutely fundamental question which cannot be shirked. It will be considered further below, but I will say at this juncture that the weight of evidence favours the view that the petiolate zygopteran wing is the ancestral type.

THE MEGANEURIDS

It is now high time to turn from general considerations to the fossils themselves. Most casual readers have heard in passing of the giant dragonflies of the Carboniferous, and tried to imagine the grand spectacle of a dragonfly two feet across flying through the luxuriant fern forest. Although the giant fossils from Commentry, in France, of Upper Carboniferous age, are the most famous meganeurid fossils, more material has in fact been found in Permian strata in Kansas and Oklahoma, and some of these fossils are not particularly large.

This early material has been authoritatively dealt with by Carpenter in several articles. In particular he re-examined the Commentry material, and sorted out a confused situation. From Commentry come two genera and four species,

Meganeura monyi, and three species of *Meganeurula*, *selysii*, *confusa*, and *titania*. *Meganeura* is ranked in the subfamily Meganeurinae, which is defined as having a long precostal space, and a proximal origin to R4+5, close to the origin of RS itself. The other genus, *Meganeurula*, belongs to the Typinae, which have a short pre-costal space, with R4+5 arising in mid-wing.

Other genera, mostly from Permian deposits in America, are *Typus*, *Megatypus*, and *Oligotypus*. A distinct and very broadwinged form, *Paralogus*, is known from the Carboniferous of Rhode Island. The meganeurids survived into the Trias, and representative fossils are *Liadotypus*, *Triadotypus*, and *Resia*.

Let us take as an example the venation of *Typus permianus* Sellards, which has provided some of the best preserved meganeurid wings. The wing is of general anisopteran form, long but relatively broad, with the same main veins as modern Odonata, namely C, Sc, R, RS, MA, CuP, and IA. The venation is very dense, with multiple distal branching of the veins, and a huge number of cells. A small basal remnant may represent CuA. There is a small pre-costal area, no nodus or stigma, and no arculus or triangle. The vein CuP is strong and markedly sinuous. IA is extensively branched, the field of branches occupying almost half the area of the wing. The venation of the other Permian fossils, for example *Oligotypus*, is very similar, while the Carboniferous fossils have even stouter veins, though similarly arranged.

In general the meganeurid wing shows its odonate lineage by the loss of MP and all but a vestige of CuA, but has none of the specializations typical of modern Odonata, in particular no nodus, stigma, or triangle. It shows specializations of its own in the extensive branching of the veins, especially IA, and in the huge number of cells.

One might imagine ways in which the meganeurid wing, especially a small one such as

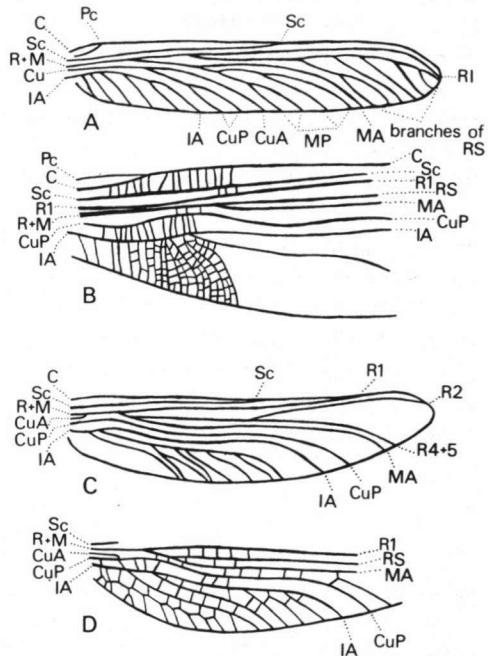


Fig. 5. Wings of Protodonata: (A) palaeodictyopteran wing (after FRASER, 1957); — (B) *Meganeurula*, (after CARPENTER, 1943); — (C) *Oligotypus*, (after CARPENTER, 1931); — (D) *Erasipteron larischi* (after CARPENTER, 1939).

Oligotypus tillyardi, only 50 mm long, could give rise to a wing of modern anisopteran form, as indeed early writers such as SELLARDS (1907) tried to do. A point of interest is that some writers have identified an oblique vein in meganeurid fossils. But there is absolutely no evidence of arculus and triangle formation, and, as we shall see later, there are more eligible candidates for the role of ancestors to the Anisoptera. The meganeurids are best considered as an offshoot from the true odonate line, exhibiting a luxuriation of venation, and ending blindly. Whether they should be given separate ordinal rank as the Protodonata, or admitted to the Odonata proper, is merely a matter of terminology.

The true ancestors of the modern Odonata must have lived alongside the giant meganeurids of the Carboniferous, but they have unfortunately left few traces. One fossil which does throw some light on this ancient stock is *Erasipteron larischi* Pruvost from the Namurien of Czechoslovakia. It is meganeurid in type with a vestigial CuA and a sinuous CuP, but without the extensive branching of the typical meganeurid and with a small total of cells. The Natural History Museum in London has recently announced the discovery of a dragonfly wing, eight inches in length, from a Derbyshire (U.K.) coalmine. An age of 300 million years has been mentioned, and if this is substantiated, it makes the fossil one of the oldest if not the oldest insect wing of any kind. The venation has not yet been formally described, but it appears to be meganeurid in character, and has been provisionally assigned to *Erasipteron*. Whether the venation is well enough preserved to justify this generic title, and whether it will shed new light on the genus, remains to be seen.

Among the Carboniferous fossils, and usually included in the order Protodonata, are two oddments, *Protagrion* and *Campyloptera*. *Protagrion audouini* has a wing much like a Palaeodictyopteran. *Campyloptera eatoni* has a petiolate wing, of simple venation, with only a few cells. MP and CuA are retained. Thus it cannot formally be considered as an odonatan. It might, and hence the attention paid to it, represent a point in the odonate line before the loss of CuA and MP. However, it is a poorly preserved fossil. Carpenter ranks it as a megasecopteran. From the point of view of nomenclature, if one removes the meganeurids from the Protodonata to the Odonata proper, then the Protodonata is left with only a few odd fossils and has no real meaning.

In general terms it is true to say that the origin of the odonate wing from the palaeodictyopteran type, involving the loss of CuA and MP, must remain in the realms of speculation. Nor can we say much about the wing which lay at the base both of the meganeurids and of the Carboniferous ancestors of the modern Odonata, until more material is available.

PERMIAN DRAGONFLIES

We now turn to perhaps the most interesting fossil dragonflies of all, small insects with simple venation, of Permian age. Those of zygopteran form are without much doubt the ancestors of the modern Zygoptera, while the place of those of anisopteran form is much less certain, providing an intriguing study.

The first of the Permian Protozygoptera, as they have been called, *Kennedya mirabilis*, was described by TILLYARD (1925a). He was examining numerous fossils which came in crates from Kansas, and the first dragonfly fossil found was the apex only of a wing. Tillyard wrote: "The keenest disappointment was felt by me for many months, while studying this wonderful find, that there should have existed, so far back as the Lower Permian, an undoubted damselfly, of which Fate had, apparently, only allowed man to reclaim the distal half of one wing. What would one not have given for the basal half with its hidden secret of quadrilateral and arculus formation! . . . At last, some 2000 specimens having been unpacked and classified, my assistant remarked to me that the sorting was just about over, as there were only about a dozen specimens left. A moment later he handed to me a specimen and its counterpart . . . I at once recognized them as the basal portion of a petiolate damselfly wing".

Subsequently a number of other Protozygoptera have been described from the Permian of Kansas and Oklahoma by Carpenter. These include other species of *Kennedya*, and the smaller genus *Progoneura*. These other fossils are similar in venation to *K. mirabilis*.

Tillyard described the wing of *Kennedya* quite clearly. It is surprisingly close to that of a modern coenagrionid. It has a petiolate base, two antenodals, a weak nodus a third of the way along the wing, and the main veins, including a weak IR2 and IR3, are disposed roughly as in the modern form. The three characters which distinguish the fossil from the modern zygopteran, and justify a new subordinal status as the Protozygoptera, are the incompleteness of the nodus, the primitive configuration of the discoidal cell, and the presence of a rudimentary basal vein between R+M and CuP, which Tillyard considered to be the remnant of CuA.

The major interest in the venation is the primitive state of the discoidal cell and arculus. A small crossvein, termed by Tillyard the medio-cubital crossvein attaches MA to CuP, and pulls down MA slightly. That is as far as things go. To make a quadrilateral all that is needed is another crossvein between MA and CuP. It is not immediately apparent whether such a crossvein would form proximal or distal to the first, but in fact as we shall see later it forms proximal, leaving the medio-cubital crossvein to be the outer edge of the quadrilateral. The second crossvein will be the lower half of the arculus, and it will attach CuP to the upper half of the arculus, which is the descending curve of R+M. The formation of a full arculus closes the discoidal cell, and *Kennedya* is thus

considered to have an 'open' discoidal cell.

If further confirmation were needed of the antiquity of the zygopteran wing, it came with the discovery of a fossil wing, *Permagrion falklandicum*, from the Permian of the Falkland Islands. This fossil was considered by Tillyard to be admissible to the Zygoptera proper. The nodus is stouter, and there is no remnant of CuA. The discoidal cell is better formed, but it is still open. The open discoidal cell has persisted into modern times in the small *Hemiphlebia* from Australia.

Three Permian fossils from Russia, described by Martynov, fall somewhere between *Kennedyia* and *Permagrion*. They all have a robust nodus and well formed open discoidal cell, but retain the remnant of CuA. They have a relatively broad stigma, which is probably why Martynov gave them lepidopteran names, *Permolestes*, *Epilestes*, and *Scytolestes*. In all these fossils, IA arises from CuP. In *Kennedyia* a little crossvein below CuP supports the end of the remnant of CuA, and Tillyard considered this to be Ac. In *Progoneura* IA is short, and there are three Ax, while all the others have two only.

Looking at these fossils it is difficult to deny that they represent a developing series tending towards the modern coenagrionid wing. NEEDHAM (1951) nonetheless dissented from such a view. He wrote: "I think that *Kennedyia* was an isolated freak in Odonata evolution that developed early and lost out entirely in the struggle for existence". He also did not like Tillyard's name CuA for the little vein between R+M and CuP, making the valid point that it seems odd to find a remnant of CuA so close to the wing base. He considered it to be the base of the anal vein, pushed under

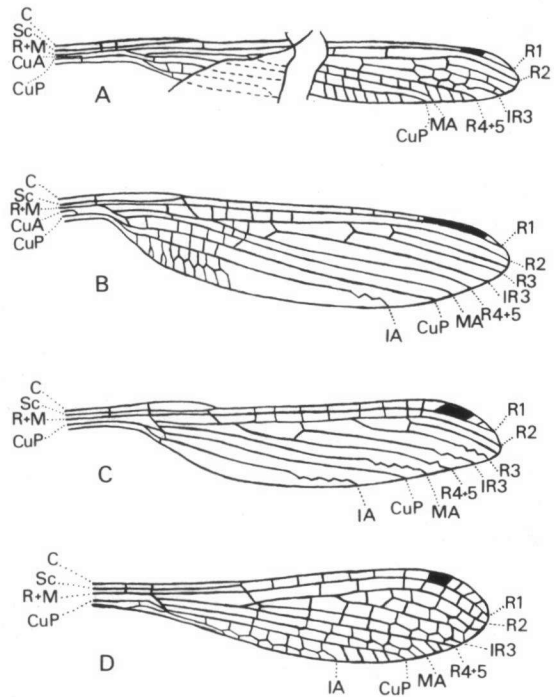


Fig. 6. Wings of primitive Zygoptera and Protozygoptera: (A) *Kennedyia* (after TILLYARD, 1925a); - (B) *Epilestes* (after MARTYNOV, 1937); - (C) *Permagrion* (after TILLYARD, 1928); - (D) *Hemiphlebia* (after TILLYARD, 1925a).

the base of the stronger cubitus by pressure from the rear.

The Permian fossils of anisopteran form are remarkable wings, and their place in the dragonfly evolutionary tree remains not absolutely clear. They consist of material from America and Australia, described by Tillyard and Carpenter under the genera *Polytaxineura* and *Ditaxineura*, and two genera from Russia, *Pholidoptilon* Zalesky and *Permaeschna* Martynov. The whole group has been given subordinal status by Carpenter as the Protanisoptera. An odd specimen from Russia, *Palaeothemis* Martynov, has a simple branching venation and is not closely related to the other fossils.

The wing of *Ditaxineura* is small, with few cells. Other salient features are a stout and oblique first antenodal, a few other non-coincident antenodals, a primitive nodus, and a wide stigma divided by the radius. There is no trace of arculus formation, but there is a medio-cubital crossvein, and a remnant of CuA. CuP is strong and sinuous, and IA is simple and relatively unbranched.

The wing of *Permaeschna* is more densely veined. It has the same divided Pt as *Ditaxineura*. Sadly the base of the wing is lost. RS runs out very straight, before the origin of R4+5 at the level of the nodus. RS and MA thus run parallel for a long way, and a crossvein joins them. There is an indentation in the hind margin where MA reaches it. Distally two veins run in the space between MA and CuP, which Martynov claimed to be the distal remains of CuA and MP.

Pholidoptilon is essentially close to *Permaeschna*, but has its base preserved. If drawn to the same scale, the two wings superimpose fairly well. It has an oblique first Ax, and no sign of arculus nor of CuA remnant. Below CuP is a triangle of veins, which ZALESKY (1931) called the triangle, but clearly it is not. The modern triangle is above CuP, and a structure below it cannot be homologous.

Discussion of this venation brings us again to the question of the origin of

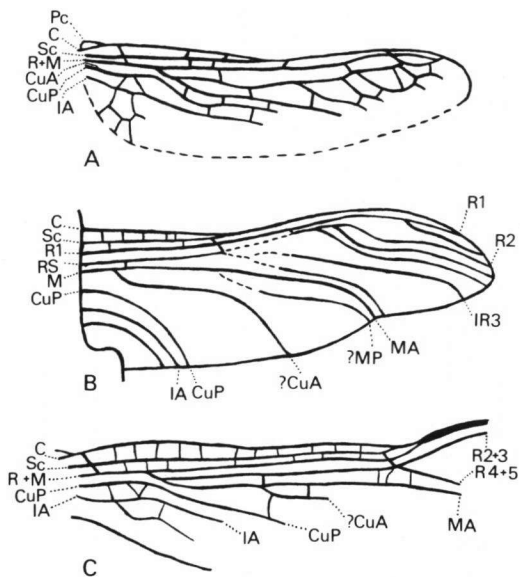


Fig. 7. Wings of Protanisoptera: (A) *Ditaxineura* (after CARPENTER, 1939); – (B) *Permaeschna* (after MARTYNOV, 1931); – (C) *Pholidoptilon* (after ZALESKY, 1931).

the modern Anisoptera. Could they have arisen from the Protanisoptera which we are considering? In his paper on *Permaeschna* Martynov states his view plainly. He wrote: "I considered to be impossible to derive the primitive and very plentiful wing-venation of Anisoptera from the very reduced venation of Zygoptera. Although Anisoptera were known from the deposits not older than the Upper Jurassic, I supposed they can be discovered in much older formations, perhaps, in Palaeozoic ones. At present, such a hypothesis has found its demonstration in the discovery . . .

of the remains of wings, belonging to the stem of Anisoptera, although more primitive, than the recent representatives of this suborder".

In favour of this idea, one can say that the wings of *Permaeschna* and *Pholidoptilon* look like anisopteran wings, and are certainly of odonate lineage, with the main veins of modern Odonata. If the distal remains of CuA and MP are retained, as Martynov suggests, then this line is older than the zygopteran one in which no trace of these veins can be found distally. The vein which Martynov designates as MP is in approximately the same position as is Mspl in the modern aeshnid. The fossil wings possess at least a primitive nodus and stigma. IA is fully developed, as it is in modern aeshnids.

On the other hand, the fossils show no trace of arculus or proper triangle. The midwing with its straight and parallel RS and MA is quite unlike any modern anisopteran. The division of the stigma by R, and the sharp downcurve of the veins immediately below the stigma, are also quite unlike modern venation.

One could readily gloss over the problems of accepting the Protanisoptera as

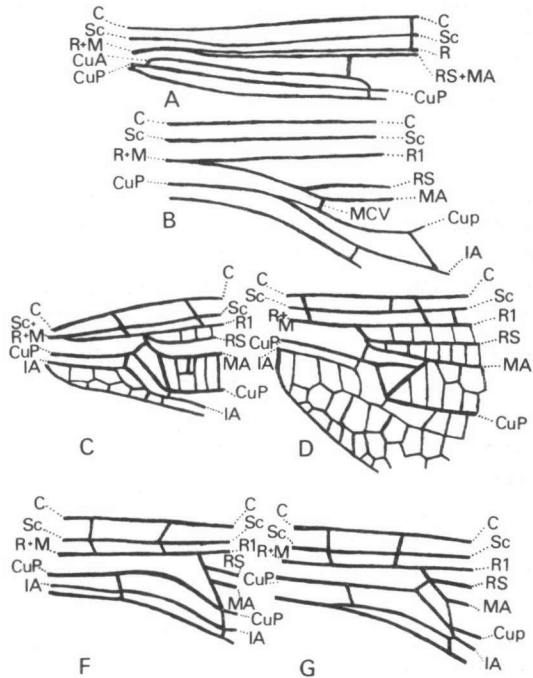


Fig. 8. Examples of arculus and triangle formation: (A) *Kennedyia*, base of wing; - (B) *Kennedyia*, medio-cubital crossvein (both after TILLYARD, 1925a); - (C) *Heterophlebia*, Fw; - (D) *Heterophlebia*, Hw (both after TILLYARD, 1925b); - (E) *Hemiphlebia*, variation at arculus and IA; - (F) *Hemiphlebia*, variation at arculus and IA (both after FRASER, 1957).

the ancestors of the modern Anisoptera were it not that in the fossils of the Lias there is evidence pointing in quite a different direction, namely to the transition of the zygopteran wing to one of anisopteran form. It is now time to examine this evidence.

THE ANISOZYGOPTERA

The most important of the fossils about to be considered are from the Lias, of Lower Jurassic age. The best known of these fossils come from Britain, and were admirably documented by TILLYARD (1925). The material consists chiefly of wings of general anisopteran shape. The term Anisozygoptera was coined by HANDLIRSCH (1906-1908) for similar fossils, and this name has stuck.

The venation of these wings is often excellently preserved and is very modern in nature. The suborder has been divided by FRASER (1957) into two superfamilies, the Tarsophlebioidea and the Heterophlebioidea. The former group includes *Tarsophlebia* Hagen, *Tarsophlebiopsis* Tillyard, *Karatawia* Martynov, *Isoflebia* Hagen, *Anisophlebia* Handlirsch, *Mesophlebia* Tillyard, *Triassophlebia* Tillyard, *Sieblosia* Handlirsch, and *Stenophlebia* Hagen. The latter includes *Liasophlebia* Tillyard, *Archithemis* Handlirsch, *Petroflebia* Tillyard, *Diastatomites* Handlirsch, *Campteroflebia* Bode, *Selenothemis* Handlirsch, *Progonophlebia* Tillyard, *Heterophlebia* Westwood, *Epiophlebia* Calvert, and *Liassogomphus* Cowley. We will not mention here the various family divisions. Most of the Tarsophlebioidea are of Upper Jurassic age, but Tillyard's *Mesophlebia* and *Triassophlebia* are from the Upper Triassic of Queensland, and *Sieblosia* is from the Oligocene. In the Heterophlebioidea, *Epiophlebia* is a recent genus, but most of the other are from the Lias. We will now go on to consider these Liassic fossils.

We will take first the venation of *Heterophlebia*. The wing is of anisopteran form, stout and fairly wide, with a relatively dense venation. There are two strong Ax, and a few weaker ones. There is a broad stigma and a well formed nodus, which joins below to R3 in an uninterrupted curve. R4+5 forks off proximal to the nodus, and IR3 runs into the fork. There are clear indications of triangle formation. CuP has a sudden downward curve. IA is well developed, and Ac is present.

In Tillyard's drawings of these wings the stages of arcus and triangle formation are seen before one's eyes. In this regard hindwing development precedes that of the forewing. In the forewing of *Liassophlebia* the discoidal cell is open, its outer edge being a long crossvein joining MA to CuP beyond the sharp downcurve of the latter, in the same position as the medio-cubital crossvein of *Kennedya*. In the forewing of *Heterophlebia* the situation is the same, except that a crossvein, the lower half of the arcus, has linked MA and CuP, before the sharp downcurve of the latter, to close the discoidal cell. In the hindwing the

final stage occurs. A strut extends from the middle of the downcurve of CuP to the point where the medio-cubital crossvein joins MA, thus 'roofing' the triangle. The modern triangle is thus complete. In most modern aeshnids, the roofing strut is stout, so that at first glance it looks like a direct continuation of the base of CuP, but in fact CuP turns down as the basal border of the triangle.

The hindwing arcus and triangle of *Heterophlebia* are so like the position in the modern Anisoptera that we can scarcely doubt that we are finally on the direct track to them. The modern Anisoptera have fully developed triangles in both fore and hindwings, and Tillyard considered that none of the Liassic fossils could be referred to the true Anisoptera, since development of the forewing triangle was not complete. In *Gomphites brodiei*, which Handlirsch placed there on the evidence of the hindwing, no forewing is preserved.

A partisan of the Protanisoptera might point out that the sharp downcurve of CuP in the forewing of *Liassophlebia* is strongly reminiscent of the anteroposteriorly elongated triangle of the modern libellulids, which are presumed to be the most advanced of Anisoptera, not the most primitive. Suppose that the Anisoptera had a dual ancestry, the libellulids arising from the Anisozygoptera and the aeshnids and gomphids from the Protanisoptera! But then we should have to suppose also that the formation of arcus and triangle occurred not once, but twice, in the course of evolution. This is admittedly not impossible, but it is difficult to believe, and there is no evidence for it.

How then does the anisozygopteran wing relate to the zygopteran line, which we left with *Permagrion* and its open discoidal cell? In the modern *Hemiphlebia*, as documented by Fraser, the discoidal cell may be open or closed. In Fraser's figures one can plainly see the very same transition as in the forewing of *Heterophlebia*, that is, the addition of a crossvein, the lower half of the arcus, to close the discoidal cell. The zygopteran discoidal cell has never developed a roofing

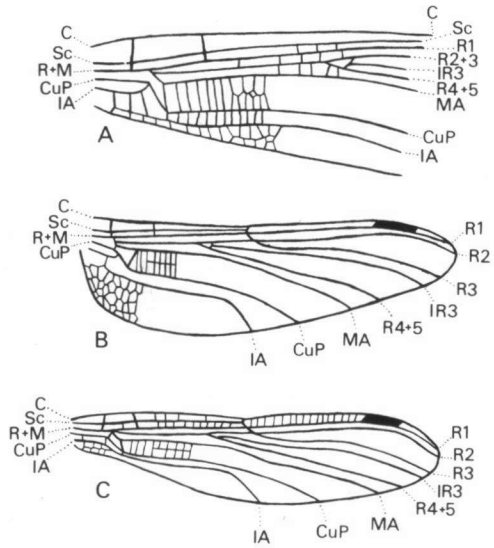


Fig. 9. The anisozygopteran wing (after TILLYARD, 1925b): (A) *Liassophlebia* Fw; - (B) *Liassophlebia* Hw; - (C) *Heterophlebia* Fw.

strut and triangle as in Anisoptera. Here at least the parting of the evolutionary ways has come. In *Heterophlebia* we have already noted the sharpness of the downturn in CuP as it forms the basal edge of the triangle to be. Among modern Zygoptera, the downturn is sharpest in the lestedids, and in the coenagrionids there is scarcely any downturn at all. Add to this the fact that in *Lestes* the stigma is long and rectangular, and IR3 and R4+5 are recessed proximal to the nodus, both anisopteran features, and the basis for the contention that the anisopteran line derives from the lested branch of the Zygoptera is clear enough.

Actual fossil evidence on the zygopteran side is extremely scanty. An important fossil is *Triassolestes epiophlebioides* Tillyard from the Upper Triassic of Ipswich, Queensland. The preservation is poor, but the discoidal cell is visible, and is closed. Tillyard figured it alongside drawings of *Epiophlebia* and *Synlestes*, remarking that in general it agrees well with *Epiophlebia*. However the fossil lacks any trace of IA basal to the discoidal cell. This makes it more zygopteran than anisozygopteran in character, and even more reduced than known Zygoptera, including the *Synlestes* with which Tillyard compared it.

There are other points in favour of this presumptive development of the anisopteran wing from a petiolate zygopteran one, via an anisozygopteran form. One of these is the possession by the anisozygopteran Liassic fossils of only two antenodals. Modern aeshnids and gomphids have two antenodals which are stronger than the others, the primary antenodals. Fraser argues for the homology of these primary Ax with the two Ax of Zygoptera. He wrote: "I took out specimens representative of the genera *Aeshna*, *Cordulegaster*, *Gomphus*, and a *Rhinocypha* and ranged them alongside one of the commoner British *Coenagrion*. Pointing to the strong antenodal veins in the wings of all the four former specimens, I asked

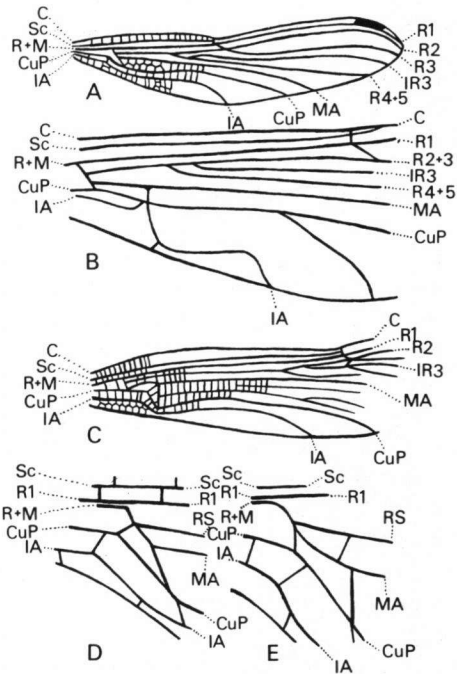


Fig. 10. Various anisozygopteran discoidal cells: (A) *Tarsophlebia*; - (B) *Anisophlebia helle*; - (C) *Stenophlebia amphitrite* (all after HAGEN, 1866); - (D) *Epiophlebia* Fw; - (E) *Epiophlebia* Hw (both after FRASER, 1957).

him (Tillyard) to compare them with the two antenodals of the *Coenagrion*, and inquired whether from the same relative position in the wing and to each other he did not think that the antenodals of all these four were homologues of those in the *Coenagrion* wing". If the aeshnids and gomphids do not descend from the zygopteran line, then why do they possess the two hypertrophied antenodals?

Another point discussed at length by Fraser is the common possession by both Anisoptera and Zygoptera of Ac. This he regards as an indication that the ancestors of the Anisoptera possessed a petiolate wing. Ac is probably present in the anisozygopteran fossils, but it is a small vein to be dogmatic about in a fossil wing. As we have seen above, Ac marks the descent of the IA trachea from its inward loop along CuP, and Fraser considered the possession of Ac in the Anisoptera as an indication that wings of this suborder descended from a wing which had undergone reduction at the base, forcing up the IA trachea, in other words a petiolate wing.

Most modern Zygoptera have no free basal portion of IA, while the Anisoptera, and the Calopterygidae among the Zygoptera, do. If no trace whatever of the base of IA were found in Zygoptera it would be rather inconvenient for our theory, since we would then have to say that a stock which had just lost the basal IA then proceeded to give rise to Anisozygoptera and Anisoptera, which have it. But in *Hemiphlebia* and for that matter in some other genera, for instance the African *Metacnemis*, the basal part of IA is clearly present, even if sometimes stuck to the hind margin in double-barrelled form. Evidently the zygopteran stock which gave rise to the Anisoptera had not yet lost the basal part of IA. This line of thought suggests that the Calopterygidae branched off from the other Zygoptera before the basal IA was lost.

The modern family Amphipterygidae is a transitional family combining both coenagrionid and calopterygid wing characters. It includes the genera *Amphipteryx*, *Devadatta*, *Diphlebia*, *Philoganga*, and *Pentaphlebia*. As an example, the wing of *Devadatta* shows the development of calopterygid characters, the addition of extra Ax, the recession of R4+5 and IR3 proximal to the nodus, and the elongation of the quadrilateral with strengthening of its outer border. There is no free basal part of IA. These forms may represent a few survivors of a transition which took place in the Triassic and Jurassic ages.

There are some oddments from the Lias which remain to be mentioned. *Progonophlebia woodwardi* Tillyard is a hindwing of anisopterian form, with a closed discoidal cell, but no triangle. R3 arises distal to the nodus, unlike most of the Anisozygoptera, in which it is bound firmly to the subnodus, and IA appears to be virtually absent. The genus *Protomyrmeleon* is represented by a wingtip from the English Lias, *P. anglicanus* Tillyard, and complete wings from Germany and Russia, *P. brunonis* Geinitz and *P. handlirschi* Martynov. The wing is petiolate. It has a greatly reduced Sc, no nodus, arculus, or quadrilateral, a full IA, and a curious conformation of veins in the distal and lower part of the

wing, where there is an abrupt change from straight veins above to markedly curved ones below. It is hard to consider it as other than a quaint offshoot from the zygopteran line. *Triassagrion* Tillyard from the Triassic of Queensland is remarkably similar.

LATER FOSSILS: GENERAL REMARKS

Most of the fossils which remain to be considered, of late Jurassic and Tertiary age, are of relatively modern form. In other words they can be referred at least to modern families, and in some cases even to genera. These fossils are numerous, in varying states of preservation, and were described piecemeal by many different workers, mostly during the last century. Thus they have been named in rather random fashion, their names often not meant to imply the close affinities with modern genera which we should like to see before employing such names today. For example a fossil named *Anax* in 1850 will probably not show the venational details required today to place it in this genus. All one might be able to say with certainty is that it is a wing of aeshnid type. Obviously, how seriously a name is to be taken depends upon the date of description, and the intentions of the describer. Some writers preferred to coin new names, to avoid the difficulty of fitting sometimes fragmentary fossils into the modern classification.

It is apparent that the whole picture is somewhat confused. Ideally re-examination of all the material would be desirable, but the fossils are widely scattered, and the task is perhaps not an especially attractive one. I am not aware that any revision has been attempted. The most comprehensive list is that of HANDLIRSCH, in his two volume book, "Die fossilen Insekten", written in 1908. Handlirsch's lists of synonymy are often long, and a later compiler might well find it necessary to make emendments. Certainly Carpenter, when revising the meganeurids, found Handlirsch's classification to be inadequate.

JURASSIC FOSSILS

The classical site for Jurassic fossils is Solenhofen, in Bavaria. The rock is marine limestone, and it must be inferred that dead insects were washed down to the shore before being fossilized. Most of the remains are not surprisingly of robust wings, yet some of the preservation is fantastically good. They are sometimes immaculately figured, especially in the work of Hagen.

There are a number of wings referable to the Anisozygoptera, within the Tarsophlebioidea of Fraser. Notable among these are *Tarsophlebia*, *Anisophlebia* and *Stenophlebia*, all figured by Hagen. Of the Jurassic fossils these are the ones least like modern Anisoptera.

Tarsophlebia eximia is a remarkable insect. The type fossil is excellently pre-

served. The body and legs are slender, somewhat calopterygid in appearance, but the venation is anisozygopteran, with an open discoidal cell, a sharp downcurve in CuP, full IA and strong R3 attached to the subnodus. There are many Ax, and it is interesting that the formation of many Ax has preceded closure of the discoidal cell in this insect. The slender legs and abdomen associated with the anisozygopteran venation is also curious, since the build of the modern *Epiophlebia* is stout, like a gomphid. An abdomen figured by Tillyard from the Lias, *Liassophlebia clavigaster*, is also stoutly formed, with segments VII-IX markedly dilated.

Stenophlebia latreillei Germar is of much more solid build than *Tarsophlebia*. The wing is broad, and the venation anisozygopteran. It has a closed discoidal cell, and narrow triangles elongated anteroposteriorly. There are many Ax. The wing of *Anisophlebia helle* Hagen is another fascinating one. It is a broad anisozygopteran wing with many Ax and a long Pt. There is a long rectangular discoidal cell, with scarcely any downturn in CuP, and the outer border of the discoidal cell is markedly strengthened. This arrangement reminds one of the modern Calopterygidae. To avoid confusion, it should be noted that these names are the ones employed by Handlirsch, and they do not always tally with those in Hagen's figures. *Anisophlebia helle* is *Isophlebia helle* in Hagen's plate, and *Stenophlebia latreillei* is *Stenophlebia aequalis* in Hagen.

One must conclude that at this period evolutionary experimentation was considerable, especially in the discoidal cell area, and in the number of Ax. At a first glance one wonders whether some of these fossils might have something to do with the Calopterygidae of today. Paradoxically the slender legs and body of *Tarsophlebia* are associated with a most uncalopterygid discoidal cell, while the most calopterygid-like discoidal cell, that

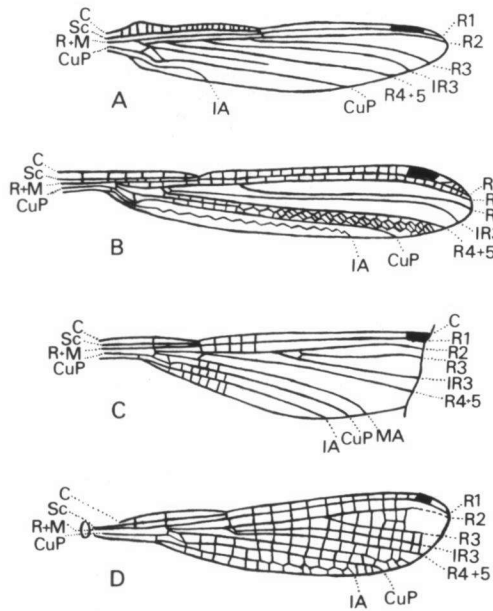


Fig. 11. Jurassic and Tertiary zygopteran wings: (A) *Euphaea*, Jurassic (after HAGEN, 1862); – (B) *Steleopteron*, Jurassic (after HANDLIRSCH, 1906-1908); – (C) *Lithagrion* Tertiary (after SCUDDER, 1890b); – (D) *Trichocnemis*, Tertiary (after SCUDDER, 1892).

of *Anisophlebia*, is associated with a very solid and powerful body. We have already discussed how in the modern Amphipterygidae there is clear surviving evidence of a smooth transition from a coenagrionid to calopterygid wing type, and it seems wisest to put the Tarsophlebioidea to one side as an evolutionary blind alley. It is nonetheless interesting to see how they experimented with the development of many Ax, and the device of strengthening the outer border of the discoidal cell, just the specializations which are found in the modern calopterygids.

The majority of late Jurassic fossils are, however, true Anisoptera. In other words they have triangles of modern types in all four wings. Handlirsch referred all those with triangles equilateral or elongated sideways to the Gomphidae, and those with anteroposteriorly elongated triangles to a new family Aeshnidiidae. The Aeshnidiidae includes two genera, *Urogomphus* and *Aeschnidium*. The latter genus is remarkable for a fantastically dense neuration, with innumerable tiny cells between the main veins. The Gomphidae of Handlirsch includes the following genera: *Nannogomphus*, *Mesuropetala*, *Protolindenia*, *Aeschnogomphus*, *Cymatophlebia*, and *Pheugothemis*.

Zygoteran remains from the Jurassic are scanty. There are only two decent specimens. *Euphaea multinervis* Hagen has a long stigma, many Ax, and R4+5 originates well proximal to the nodus. There is a sharp inflexion in the costa near its base. The discoidal cell is not unlike the modern Polythoridae. *Steleopteron deichmulleri* Handlirsch has been carefully re-examined by Fraser, who removed it from a special family created for it by Handlirsch to the Amphipterygidae. *Steleopteron* has several Ax, a coenagrionid type discoidal cell, no free basal IA, and R4+5 and IR3 originate proximal to the nodus.

It remains to mention some larval forms described by Brauer et al. (1889) under the name *Samarura*, with the perhaps unduly generous application of five specific names. These nymphs have long cylindrical abdomens and three broad leaf-like appendages. Handlirsch referred them to the Anisozygoptera, but the nymph of *Epiophlebia* is distinctly anisopteran in form, so that unless they belong to species within the Tarsophlebioidea it seems unlikely that this is the correct explanation.

TERTIARY FOSSILS

Lastly we come to the Tertiary fossils. Almost all of these are of modern form, and in some cases have been compared in detail by their describers with extant species. As with the Jurassic fossils, no attempt is made here at a complete list. The two places which have yielded good series of fossils are Florissant, in Colorado, of Oligocene age, and Oeningen, in Baden, Germany, of Miocene age. These fossils are known chiefly through the work of Scudder at Florissant and Heer at Oeningen. Corbet has argued back from the fossils to

conclude that the Florissant site represented a high altitude lake, populated chiefly by coenagrionids and aeshnids, while Oeningen was lower lying, with many libellulids among the fossils. Other sites worthy of mention are the Green River, Wyoming, of Oligocene age, Sieblos in Bavaria of middle Oligocene age, and Rott im Siebengebirge in the Rheinland, of Upper Oligocene age. Apart from these sites, there are single fossils from other places.

The zygopteran fossils described by Scudder and Heer were given names varying on the term '*Agrion*'. Without attempting too much precision, we can say that they are all coenagrionid in venation, with IR3 arising at the subnodus, and a coenagrionid type of discoidal cell. Some of them have rather broad stigmas. Scudder's genera from Florissant include *Agrion*, *Lithagrion*, and *Trichocnemis*. From the Green River come *Dysagrion* and *Podagrion*, which has only the apex preserved. For the coenagrionid fossils from Oeningen, Heer uses the generic title *Agrion*. Hagen's *Agrion myasis* from Rott im Siebengebirge is coenagrionid, while his *Lestes vicina* from Sieblos has IR3 arising proximal to the nodus, and can thus be accepted as lested in the modern sense. *Eothaumatoneura* Pongranz is described by its author as a calopterygid wing fragment.

Turning to the Anisoptera, aeshnid and libellulid fossils predominate. From Florissant come *Aeshna solida*, *Basiaeschna separata*, and *Lithaeschna. Petalura acutipennis* Hagen from Sieblos has a very long thin stigma, and an elongated triangle. There are some libellulid wings, notably *Libellula perse* from Oeningen, and *Libellula cellulosa* from Rott im Siebengebirge. Most of the libellulid fossils are however nymphs, from Oeningen and Rott im Siebengebirge.

From Rott im Siebengebirge comes *Ictinus fur* Hagen, which has a clearly gomphid wing base with triangle and subtriangle both crossed. *Croato cordulia*

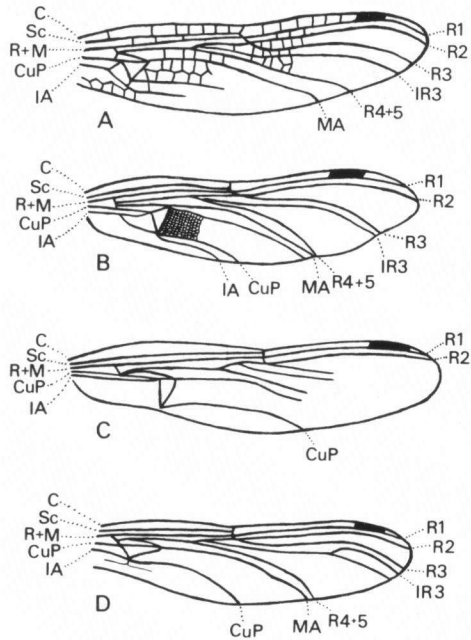


Fig. 12. Jurassic and Tertiary anisopteran wings: (A) *Nannogomphus*, Jurassic; – (B) *Aeshnidium*, Jurassic (both after HANDLIRSCH, 1906-1908); – (C) *Libellula*, Tertiary (after HAGEN, 1863); – (D) *Aeshna*, Tertiary (after SCUDDER, 1890b).

platyptera (Charp.) and *Stenogomphus carletoni* Scudder were both described as corduliids, though Needham says that *Stenogomphus* is a libellulid. There remains to mention *Siebloisia jucunda* Hagen, which is an anisozygopteran. It has a closed discoidal cell, but no true triangle. Hagen called it *Heterophlebia*, but Handlirsch created a new genus for it.

CONCLUSION

We have now completed our armchair survey of fossil dragonflies. First we considered the great meganeurids from Commeny and their Permian brethren from America, a remarkable blind alley in odonate evolution. Then came the simple Protozoptera, ancient forerunners of the modern Zygoptera. Equally ancient are the Protanisoptera, and we mentioned the arguments for and against them being ancestral to modern Anisoptera. In the next section, concerning the Liassic Anisozygoptera, we discussed the evidence in favour of the transition from a petiolate wing to one of anisopteran form, and were able to follow the steps in arculus and triangle formation in the fossil wings. Lastly came the fossils of the Jurassic and Tertiary ages, mostly close to modern dragonflies, excepting the bizarre anisozygopterans.

If based on the conclusions arrived at above, an evolutionary series for the dragonflies would read something like this: palaeodictyopteran-like ancestor; first odonate form, lacking MP and CuA, something like *Erasipteron larischi*; Protozoptera; *Permagrion*; coenagrionid; lestad; *Heterophlebia*-like anisozygopteran; Anisoptera with primary Ax; Anisoptera without primary Ax. This scheme places the libellulids at the apex of the evolutionary line. It means that the main side branches are the meganeurids, the Protanisoptera, the Tarsophlebioidea, and the Calopterygidae, with several minor branches among the modern Odonata.

In this story perhaps the most remarkable thing is the evolutionary conservatism which has kept the coenagrionid wing in almost the same simple form since the Upper Permian, throughout 200 million years during which vast changes took place in the natural history of the earth. Perhaps in another 100 million years the coenagrionid wing will still exist, while the other two great modern lines, the anisopterans and the calopterygids, may be gone.

In the Introduction the question was raised which venational features were primitive and which specialized. After following the twists and turns of the story, the reader will appreciate that statements on this subject depend upon what evolutionary series one believes in, and that a clear distinction must be made between wings which are simply old, and those that are primitive. The meganeurid of the Carboniferous is in some ways more specialized than the coenagrionid of today, but in others more primitive. The meganeurid has a specialized luxuriation of venation in its multiply-branching veins and many

cells. On the other hand it has no arculus or discoidal cell. Only if one chooses to weight these characters unequally can one say which form is the more primitive.

Nonetheless a number of comparative statements can be made. Simple venation with few cells is more primitive than luxuriant venation with many cells. A venation with tidily ordered crossveins is more advanced than one where the crossveins are non-coincident. The possession of a nodus and a discoidal cell is more advanced than their absence. A closed discoidal cell is more advanced than an open one, and a triangle still more advanced. Forms in which the origins of R3 and IR3 are linked to the subnodus are more specialized than those with distal origins to these veins, and the regression of R3 and IR3 proximal to the nodus is more specialized still. A form with two Ax is more primitive than one with more. An anisopteran wing which has retained two primary Ax is more primitive than one which has lost them.

It is worth considering at what points new evidence would be most valuable, and where the story might have to be re-written. The earliest steps, the development of an odonate wing lacking MP and CuA, the branching off of the meganeurids, and the origins of the Protozygoptera, all need clarification. There are many points in favour of the origin of the anisopteran wing from a petiolate form, but more fossil evidence of the Triassic and Liassic Zygoptera would be very valuable. And if a meganeurid or protanisopteran wing were to be found which did possess evidence of nodus, arculus, or triangle formation the whole question of the origins of the Anisoptera would be re-opened. Finally, more Jurassic Zygoptera and Tarsophlebioidea material would be interesting, to clarify the relationships between what are at present rather isolated fossils, and to document better the earliest calopterygids.

There may still be some living fossils to be caught among the recent Odonata. If the beginning reader should have the good fortune to net one, I hope that this article may have helped him to recognize the fact. I hope too that it may provide a useful base from which to approach the writings of the giants of the past, especially Needham, Tillyard, and Fraser, with all their vast experience of the order. At one time discussion of the relative merits of the Comstock-Needham and Tillyard systems of notation became rather heated. For instance, NEEDHAM (1951) stated: "Tillyard left behind him a system that does not make sense, encumbered by vein-labels so bungling that his own followers get confused in using them." The Tillyard system found an able champion in Fraser, who in turn vigorously attacked the theory of pre-tracheation. While the beginning odonatologist must decide for himself which notation he prefers to use, he should not be put off by the old atmosphere of controversy, and there is much enjoyment to be had in thinking about a subject which is neither as dry nor as certainly worked out as may at first appear.

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* The list offered is only a selection. Other cross-references are easily found in the excellent articles by CARPENTER (1931-1953) and TILLYARD (1914-1938), while for the confused assemblage of writings on Jurassic and Tertiary forms, a good source is HANDLIRSCH's (1906-1908) book. Almost complete bibliographic catalogues have been published by SCUDDER (1890a) and RODENDORF (1962).

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