

A RECLASSIFICATION OF THE ORDER ODONATA.
BASED ON SOME NEW INTERPRETATIONS OF THE VENATION
OF THE DRAGONFLY WING.

By R. J. TILLYARD, M.A., Sc.D. (Cantab.), D.Sc. (Sydney), F.R.S., F.R.E.S.†

WITH NOTES, PREFACE AND COMPLETION THEREOF.

By F. C. FRASER, Lt.-Col. I.M.S., Retd., M.D., M.R.C.S., L.R.C.P., F.R.E.S.

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The captions at the top of the right-hand pages from 127 to 161 should be "Tillyard and Fraser."—Ed.

References and material, or to accepting statements published by other authors at their face value.

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In undertaking to complete the paper, three courses were open to me—firstly to publish the MS. as it stood, a procedure which was open to the objection that certain serious errors, which it contained, might mislead the student. Secondly, to publish a corrected edition of the paper, giving a series of footnotes, pointing out where corrections had been made and the reasons for making them. Thirdly, to rewrite the paper entirely and assume joint responsibility for the views set forth therein. Such a procedure would have been unfair to the original author who would, now, not be able to disavow any fresh views which I might include; moreover, I was not prepared to accept a joint responsibility, since in some respects I did not see eye to eye with Dr. Tillyard. Thus I have elected to steer the

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PREFACE.

The untimely and tragic death of Dr. R. J. Tillyard in the early part of 1937, not only ended the career of a great scientist but robbed Entomology of much valuable knowledge which it might have acquired through the research work of one of its greatest students.

Among several valuable papers which Dr. Tillyard was engaged upon at the date of his death, was one dealing with a New Classification of the Order Odonata. This was to have been published in three parts, of which the first two had been practically completed.

Non-publication of this work would have been a loss to science; posthumous publication would be the best tribute to its author's memory. For these reasons, and because I had kept in close touch with him during its writing, both by correspondence and exchange of views, I have undertaken the responsibility of completing it and seeing it through the press.

At the outset, I was beset with certain difficulties, for a careful perusal of the MS. revealed a number of errors, one at least due, I think, to a *lapsus calami*, but sufficiently misleading as to be serious; others due to lack of references and material, or to accepting statements published by other authors at their face value.

The early part of the paper deals with venational problems and puts forward some new interpretations of these; the latter part bears more on classification but as of secondary importance to evolutionary problems, for the writer aptly says, that the problem of correctly classifying this enormous complex of forms is a purely secondary matter which can best be undertaken as a separate study by somebody with more first-hand knowledge of non-Australian forms than he can ever hope to obtain. For this reason, I have altered his title of the paper to one which is in more accordance with its subject matter. (Originally it stood simply as: "A New Classification of the Order Odonata".)

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middle course and, whilst emending such passages as were likely to mislead the raw student of the Order, I have added explanatory notes to show where this has been done. Such footnotes have been kept down to a minimum, since it seemed more desirable to leave criticism, if any, to come from other quarters.

Although Dr. Tillyard's paper remains so lamentably incomplete, it is abundantly clear from so much of it as has been written that he had jettisoned his former theory that the whole of the Order Odonata has evolved from a simple-winged zygoterous type, in favour of one put forward by Professor Carpenter, which holds that the two suborders Zygoptera and Anisoptera have had independent origin from zygoterous and anisopterous types respectively.

This was extremely characteristic of his temperament, for he held that unless we were prepared to abandon the discredited theories of yesterday, science could hope for no advance on the morrow, or, at the least, it would be hampered in its advance. "I am no believer in Lost Causes", he wrote to me on one occasion.

Nevertheless, I have still sufficient faith in Dr. Tillyard's interpretations of the wing venation of the Odonata, especially of those relating to the remarkable changes which have taken place at the base of the wing, as to believe that he has been too precipitate in abandoning his former theory. I believe, and I shall attempt to show in Part II of this paper, that Professor Carpenter's epoch-making discoveries in the Permian beds of Kansas have been unduly overrated.

In the present Part I have called attention to structures in the costal border of the wing made up of the Costa, Subcosta, Radius and the two primary antenodal nervures, a complex which I call the "Costo-antenodal". A study of this has convinced me that it is of great phylogenetic importance and that the two antenodals are among the earliest structures evolved in the dragonfly wing. Whilst great importance can be placed on the structure of the primitive fossil wing, an equal reliance on vestigial structures existing in the wings of recent forms is necessary, since the two are complementary to one another.

I desire here to acknowledge much valuable assistance given me by Mr. John Cowley, especially in regard to the listing of genera and to the synonymy involved.

F. C. FRASER.

Bournemouth, Hants.

INTRODUCTION.

The oldest known winged insects, or the Pterygota, come from the Upper Carboniferous of Europe and North America. They fall into two types, viz., the Palaeoptera, a group of Orders characterized by their inability to fold their wings backwards so as to form a roof over the abdomen, and the Neoptera, another group of Orders in which the wings were, when in the position of repose, folded back in such a manner, thus forming a protective covering for the abdomen which was weakly chitinized in contrast to the tough, strongly chitinized head and thorax. To the Palaeoptera belonged the fossil Orders Palaeodictyoptera, Megasecoptera, Protodonata and Protphemeroptera; to the Neoptera, the fossil Orders Protoblattaria, Protorthoptera and the still existing Order Blattaria which was dominant in the Upper Carboniferous.

The only Palaeopterous Orders existing at the present day are the

Plecoptera or Mayflies, and the Odonata or Dragonflies. They stand far apart from one another, but much farther apart from all other existing insects. In contrast with the early success and almost constant form and venation of the Cockroaches (Order Blattaria), the Mayflies and Dragonflies exhibit a surprisingly changing ancestral history and the present-day types in both Orders were not attained until the Upper Jurassic or later. In the case of the Mayflies, the evolutionary changes involved heavy reduction of the size and venation of the hindwing, with complete loss of mouth-parts in the adult insect. Thus the struggle for existence was for the most part transferred to the larvae, which therefore, at the present day, offer us characters of greater value in classification than do the adults. In the case of the Dragonflies, the fore and hind wings remained in the primitive condition of being equal in size and similar in venation in all the more primitive (Zygopteroid) types. But a new line arose in the Jurassic in which the hind wing became more specialized than the fore, and also tended to become somewhat broader; these were the larger present-day types called Anisoptera.

The fossil record shows that the evolutionary ancestry of the Dragonflies is unexpectedly complex. Lameere, through a brilliant analysis of the old Order Palaeodictyoptera, and an equally brilliant concept of the original, ancestral type of venation, has laid the foundation of a sound understanding of the evolution of both the main groups of Palaeoptera; these he called the "Ephemeroptera" and the "Odonatoptera". Since, however, the ending "ptera" is used in the Class Insecta to indicate groups of the rank of Orders, and Lameere's groups have the rank of Superorders, I must change the name "Ephemeroptera" to "Plectopteroidea", indicating a Superorder consisting of Orders allied to the Mayflies or Plectoptera, and the name "Odonatoptera" to "Odonatoidea", indicating a Superorder, consisting of Orders allied to the Dragonflies or Odonata.

THE VENATION OF THE PALAEOPTEROUS ORDERS.

Because most of the fossil insect-remains known to us are wings, the study of insect evolution resolves itself chiefly into a study of the evolution of various types of wing-venation. The vast knowledge of new types of fossil insect wings accumulated since the publication of Comstock's famous book ("The Wings of Insects", 1918) has shown conclusively that his hypothetical ancestral type of wing-venation is by no means an old type geologically, and that a much older and more complete hypothetical type is needed if we are to understand the venations of more archaic orders. Comstock failed to appreciate the earlier work of Audouin with its insistence on the importance of alternating convex and concave veins. But it is just in the older types of insect wings, and more especially in the Palaeoptera, that this alternation of convex and concave veins is found to be of the utmost importance. Indeed, it may confidently be asserted that, as long as the wings retained their primitive position of being held, when at rest, free from the abdomen without being folded roof-wise above it, so long did the primitive alternation of convex and concave veins remain unchanged, even when one or more of the original main veins had been eliminated.

In order to understand the venation of the Odonata, we must first of all be perfectly clear about the ancestral Palaeopterous type postulated by Lameere. According to Lameere, each vein arising from the base of the wing originally divided into two branches, an upper or anterior convex and a lower or posterior concave one. There are five separate veins at the base

of the wing, viz., the Costa, Radius, Media, Cubitus and Analis. Each of these except the anal, divides into another convex and posterior concave main veins, according to the following Table:—

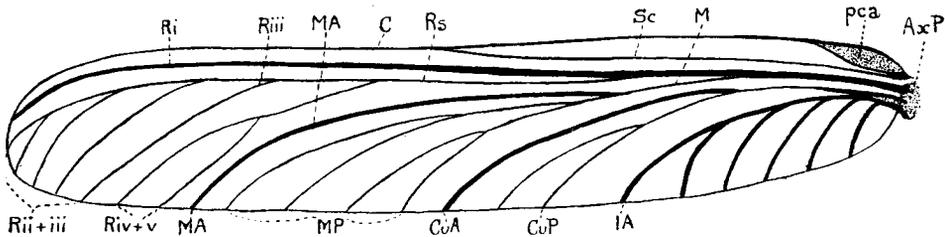


Fig. 1.—*Dictyoptilus sepultus* Handl.

Table of Alternating Convex and Concave Veins in Palaeopterous Orders.

Basal Vein.	Main Logitudinal Vein.	Type.	Ideal Notation.	Usual Notation.
COSTA.	Costa.	Convex.	CA.	C.
	Subcosta.	Concave.	CP.	SC.
RADIUS.	Radius.	Convex.	RA.	R.
	Radial Sector.	Concave.	RP.	Rs.
MEDIA.	Anterior Median.	Convex.	MA.	MA.
	Posterior Median.	Concave.	MP.	MP.
CUBITUS.	First Cubitus.	Convex.	CuA.	Cu1.
	Second Cubitus.	Concave.	CuP.	Cu2.

This arrangement is well shown in the genus *Dictyoptilus* (Fig. 1).

Comstock failed to recognize the existence of the anterior median, MA, and thus his hypothetical type included only the concave posterior branch of the ancestral median vein. He also failed to homologize correctly the two main branches of the Cubitus in various Orders, paying no attention whatever to the convexity or concavity of the main veins, and selecting as his Cu2, in certain Orders, the vein which we now know to be the convex first anal (1A).

The anal veins present a special problem which I do not think has yet been fully solved. No type of wing is really known, even amongst the oldest fossils, where a true concave anal vein exists. In those Palaedictyopterous and Plectopterous wings in which the basal connections of the anal veins can be clearly seen, it can be established beyond doubt that any concave veins present in the anal region are of the type known as "intercalated" or "triadic" veins.

In the present state of our knowledge, we can recognize three types of structure in the anal region of the wing, as follows:—

- (1) The oldest type, or Plectopteroid, in which, instead of a true third axillary at the base of the wing, there is a series of weakly chitinized plates constituting the *posterior axillary region*; from

these are developed a varying number of convex anal veins, of which the first two at least (A1 and A2) are separated by a concave intercalated vein, the inter-anal, 1A1.

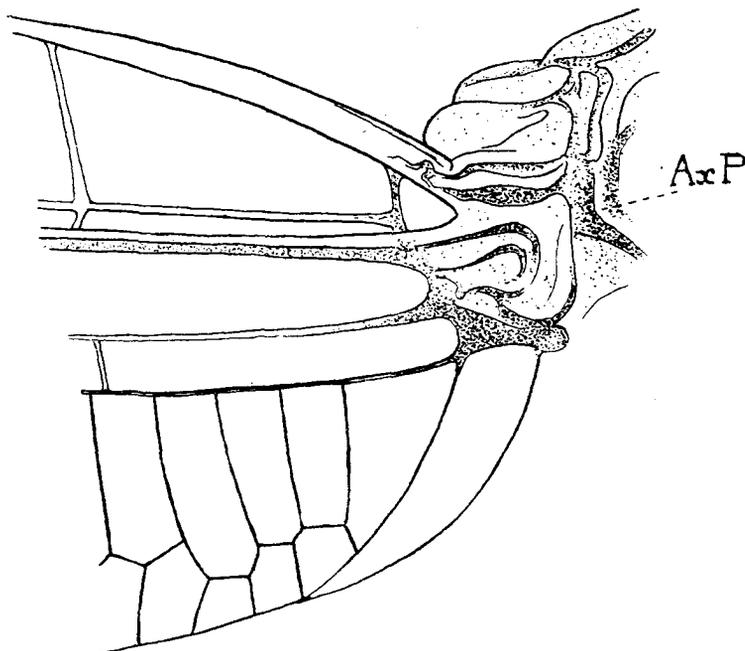


Fig. 2.—Odonatoid type of wing; base only shown. *AxP*. Axillary plate.

- (2) The Odonatoid type, in which the weakly chitinized plates found in the older Plectopteroid types are replaced by a single stoutly chitinized *axillary plate* (*AxP* in Fig. 2) to which are attached *all* the posterior veins of the wing, viz., the Radius, Media, Cubitus and Anal.
- (3) The Neopteroid type, in which the original series of weakly chitinized plates found in the Plectopteroid type is replaced by a set of three strongly chitinized and distinct axillaries, (1Ax, 2Ax and 3Ax). The whole of the anal veins in the Neoptera appear to have been evolved in intimate relationship with the third axillary (3Ax), and all the anal veins present are always convex veins. From a study of fossil types, I am of opinion that there are only two anal veins originally in the Neoptera, viz., 1A and 2A (or, if preferred, A1 and A2). The so-called third anal (3A) of Comstock can be clearly seen in such ancient Orders as Protoperlaria, to be nothing else than a posterior convex branch of 2A. If, therefore, we continue to use the notation 3A, we must always remember that it is only for convenience and that this vein, and 4A when present, are only branches of the second anal vein.

Reviewing the above evidence, we see that the most ancient type of

all, the Plectopteroid, could very well be the ancestral type for the whole of the Neoptera. At the present day, these latter form the great majority of winged insects and include all the existing Orders of Pterygota except the Mayflies and Dragonflies. But the Odonatoid Orders form an evolutionary side-branch from the Plectopteroid type, characterized by great strength of wing-veins and wide-membrane by the locking together of all the main veins of the wing except the costa, through the development of the strong unyielding *axillary plate*. In other words, while it is true that the Mayflies and their ancestors could not flex their wings so as to fold them roofwise over the body, yet the basal mechanism of this kind of wing was of such primitive type that a flexor mechanism could still have been developed. In the Odonata and their ancestors, specialization has proceeded too far to allow of this latter possibility; thus we note that when, at a later stage, types of dragonflies were evolved in which the wings could *apparently* be folded back along the abdomen, this position was not achieved by flexing the wing at all, but by evolving an obliquely placed thorax and retaining the original method of folding the wings vertically above the body! Correlated with this condition of the wings, we find a single posterior axillary plate (AP) and a single convex anal vein. As this vein is almost certainly the homologue of the first anal of the Mayflies, it is here named 1A.

THE ODONATOID TYPE OF VENATION.

It is only in the Plectopteroid groups that the original costal vein C or CA remains distinct from the costal margin of the wing. In all Neoptera it has disappeared entirely, or perhaps we should say that it has become merged in the costal margin. In the Odonatoid Orders, we find, in the oldest types, a hardened *precostal area* (Figs. 1, 4 5) which appears to represent a secondary margin and the costal vein near the base of the wing. Even in some modern types, e.g., *Petalura* and *Sieboldius*, a remnant of this area can still be recognized, but in most forms, it is merely represented by a thickening of the costal margin basally

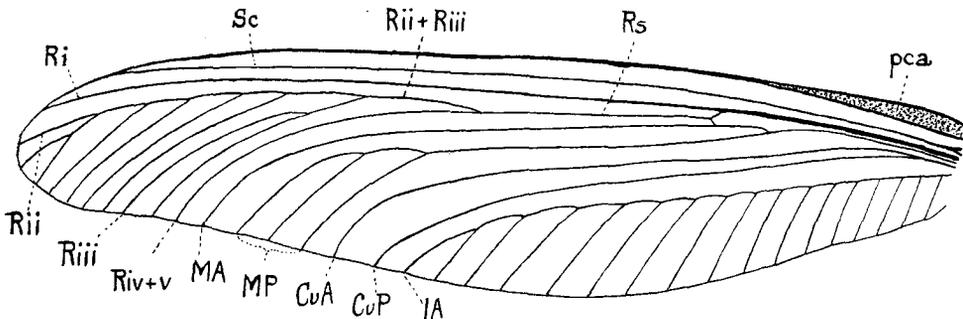


Fig. 3.—*Protagrion audouini* Brong.

Both in the Plectopteroid and Odonatoid groups, the original type of branching of the radial sector is altered by the addition of intercalated sectors. The original type of branching is that found in the Palaedictyoptera, viz., a series of descending branches arranged pectinately (Fig. 1). All these branches are concave veins. In the oldest types, Rs.

divided not far from its origin into $R2 + 3$ and $R4 + 5$, but further additional branches were only added to the former, leaving $R4 + 5$ as a simple vein throughout the whole series. In all but the oldest groups of Odonatoidea, the branches of $R2 + 3$ become standardized into two true concave branches, $R2$ and $R3$, and two intercalated sectors, $1R2$ and $1R3$, both of which, of course, are convex veins (Fig. 8).

Originally, both in the Plectopteroidea and Odonatoidea, R_s was quite separate from MA . But very early in the evolutionary history of both groups, the basal portion of MA became obsolete and this vein then became completely attached to R . The composite vein so formed is labelled $R_s + MA$ in most figures in this paper.

The Nodus.

Except in some of the earlier fossil types of Odonata, we meet with a specialization in the form of the subcosta, which becomes more or less shortened and meets the costa in a more or less specialized manner at the nodus ("N" in figures). In all living types of Odonata, the costa is flexible at the nodus, (i) and this flexibility gives the insect increased powers of flight. The history of the evolution of the nodus, as shown in the fossil record, indicates that it was at first nothing more than the upturned end of the subcosta, $Sc.$, meeting the slightly downwardly bent costa, as in *Kennedya* (Fig. 6). But already, as in *Kennedya* there were cross-veins situated near the nodus, both proximally and distally. The next step was for one set of cross-veins, consisting of a nodal veinlet (nv) and a subnodal veinlet (snv) lying below it, to approach the nodus more closely and to become obliquely placed so as to form a strut beneath the end of Sc . This stage is well shown in *Permagrion* (Fig. 7). To attain the present-day form of nodus, it was only necessary for the supporting strut to move close enough to the nodus to leave only a very short projecting end of Sc . beyond them; this portion then became strongly upturned, often almost at right-angles to the costa, while the angle between it and the nodal vein below it became more and more obtuse. The subnodal veinlet also became strengthened to form the subnodus (Fig. 7, *sn.*), (ii).

The Pterostigma.

Another important specialisation found in most Odonata is the pterostigma (*pt* in figs.). This is a more or less strongly chitinized area

(i) Dr. Tillyard is surely incorrect here : the nodus is not a joint and can hardly be designated as a "pseudo-joint". I have put a few wings to the test by attempting to flex them at the nodus and find that the costal border first of all goes into a spiral twist, then buckles and finally snaps off at the distal side of the nodus. Actually the nodus represents the distal end of the costoantennodal complex which I describe fully in footnote (ii) and from it are splayed out the apical portions of the wing. A joint in this position would result in a flapping, helpless wing, since without musculature, it would buckle at every stroke. Fraser.

(ii) *The Costoantennodal Complex* (Fig. 11).

With the formation of the nodus, the three nervures Costa, Subcosta and Radius become strongly bound together proximally and distally and this union is further strengthened by two antenodal nervures which are situated nearly midway between the nodus and base of wing and a short distance from one another. These antenodals are formed by two short

situated between costa and radius, somewhat before the apex, at the region of greatest impact of the wing on air during flight. Originally it appears to have covered only a single cell, i.e., the space between two consecutive cross-nervures, but in some of the most heavily veined recent forms it may cover a space equivalent to a number of small cells. In a few forms (e.g., the Pseudostigmatidae), (Fig. 20), it becomes hypertrophied or abnormal, while in others (males of some Agriidae) it is obsolete.

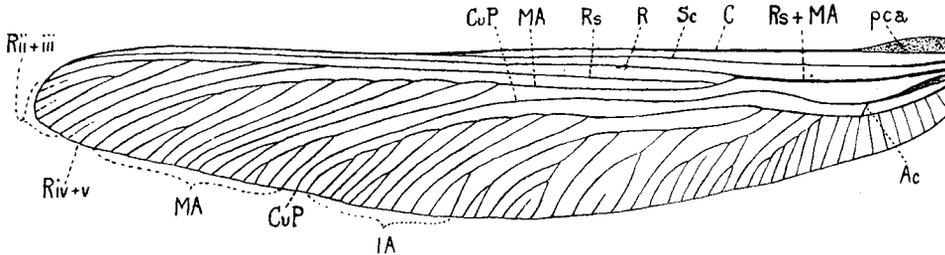


Fig. 4.—*Typus permianus* Sell. Forewing.

The Arculus.

The most important specializations in the wings of Odonata occur in the region of the *arculus* (Figs. 7, 9b). We have mentioned already that, in almost all Odonata, the original stem of MA has been lost, so that this vein becomes attached secondarily to Rs. The arculus may be defined as the free basal portion of Rs + MA after it leaves the common stem with R, together with any supporting cross-vein beneath it. In recent forms (Fig. 23) the complete arculus consists of two parts, viz., the *anterior arculus* formed from the strongly bent basal portion of Rs + MA, and the *posterior arculus* formed from a specialized cross-vein below it. The fossil record shows how this specialized form of complete arculus arose. There is, first of all, as in *Kennedyia* (Fig. 9B) and *Ditaxineura*, only the oblique weakly specialized free basal portion of Rs + MA, without any supporting cross-vein below it; the cross-vein that comes nearest in position at this stage is the discoidal cross-vein, *dv*, (Fig. 9), which is destined to play an entirely different part, as we shall see when considering the evolution of the discoidal cell or quadrilateral. Consequently, in some primitive

cross nervures which run from the Costa and Radius to meet at the same point on the Subcosta, and since the latter is concave to the Costa and Radius, the two halves meet at an angle. Moreover the costal plane or space enclosed between the Costa and Subcosta, is at an angle to the subcostal plane, or space between the Subcosta and Radius, so that the whole structure is one of great strength and resembles an angle-iron girder reinforced by two strong angle-irons at its centre. The two antenodals are known as the "primaries", since they are found in the earliest known fossil wings of dragonflies (Fig. 6); later we shall see that they are joined by other, weaker antenodals, the two halves of which fail to coincide, known as "secondaries"; and later still in evolution, the primaries are entirely replaced by the secondaries, a stage which represents the highest point of evolution attained by the Order. The whole structure composed of Costa, Subcosta, Radius and the two primary antenodals is known as the "Costoantenodal complex". Fraser.

types, we find that the arculus is *incomplete* (e.g., *Permagrion*, *Permolestes* and forewings of *Hemiphlebia* and *Chorismagrion*). Later, a cross-vein became developed beneath the anterior arculus, and this not only completed the arculus itself, but at the same time turned the open space below it into a closed quadrilateral (iii).

The Discoidal Cell.

Of all areas in the Odonate wing, the discoidal cell (*dc*), (Fig. 14), is the most important and most highly specialized. We have seen in the preceding paragraph, that this area was not originally a closed cell, and that it still remains open in the forewings of two living genera of dragonflies (*Hemiphlebia* and *Chorismagrion*). In all other living types, it is completely closed and either entire or divided. It lies between the free basal piece of MA above and the somewhat curved or bent portion of CuP below; its proximal side is the *posterior arculus*, and its distal side, often very obliquely placed, is the original *discoidal cross-vein* (*dv*) (Fig. 9B). A study of fossil forms will easily convince us that the predetermining factor for the formation of this cell was simply the curious sigmoidal curvature of vein CuP in the region of the arculus whereby the evolution of a cell of specialized form was rendered possible.

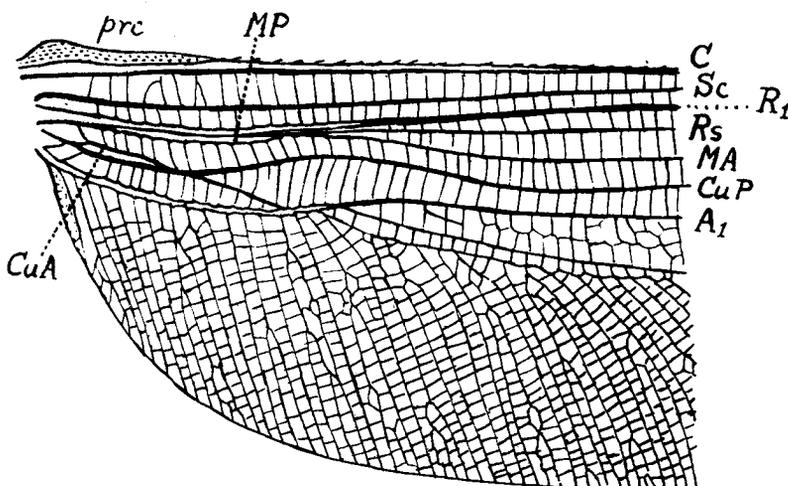


Fig. 5.—*Megatypus schucheri*.

In all Zygopteroid types, the discoidal cell remains a quadrilateral. In some Anisozygoptera of Mesozoic times, the hindwing outran the fore

(iii) The level of the arculus in primitive forms is slightly distal to the level of the distal primary antenodal nervure. As we trace evolution upwards, towards recent forms, it is seen that the level of the arculus becomes recessed towards the base of the wing: at first at and in line with, the distal antenodal, then at a level midway between the two antenodals and finally, in many recent or present-day forms, it actually lies nearer to the level of the proximal antenodal. Thus the level of the arculus is of primary importance in estimating the stage of evolution reached. Fraser.

in specialization, so that we find forms in which the forewing retained the quadrilateral while the hindwing built up a much more specialized subdivision of this cell into a triangle-plus-supratriangle. In the true Anisoptera, the original quadrilateral is subdivided into triangle-plus-supratriangle in both fore and hind wings. (The Anisozygoptera and Anisoptera will be dealt with more fully in a later part of this paper).

The Subquadrangle.

The only other specialized region now remaining to be considered, is that known as the subquadrangle (*sq* in figs.) lying below the quadrilateral in the region between CuP and 1A. The subquadrangle has ceased to be of much importance in the study of modern types, yet when we look at the earlier fossil forms, we are surprised to find that it existed in the form of a completely closed cell well before the time when the discoidal cell itself became closed, e.g., in *Kennedyia* (Fig. 9B), *Permolestes* (Fig. 8), and *Permagrion* (Fig. 7). There can be no doubt that in these three fossil forms, veins CuP and 1A were fused basally; the subquadrangle is formed as the first enclosed cell after CuP diverges from 1A below the region of the arculus. But in the Hemiphlebioidea (Hemiphlebiidae) we meet with the older arrangement in which the vein 1A remains distinct from CuP throughout; instead, it is basally fused for a greater or less distance with the posterior border of wing. On the Anisoptera, an even more primitive arrangement is retained, viz., that veins CuP, 1A and the posterior margin of wing are all separate and distinct from the base of wing outwards (iv).

The Anal Crossing.

The above differences have not been understood clearly up to now, and hence there is some ambiguity in the use of the term *anal crossing* for the cross-vein which connects CuP with the posterior margin of the wing near the distal end of the petiole in Zygoptera. This cross-vein is laid down along the course of the anal trachea of the nymphal wing, and therefore the term *anal crossing* (*Ac*), which I originally gave it, must be strictly understood to apply to this fact only; it must not be concluded that the anal vein also always follows this course. It does so, obviously, in *Kennedyia*, *Permolestes* and *Permagrion*. In *Hemiphlebia* (Fig. 13) the anal vein can be followed as a distinct vein from the base of the wing, lying in contact

(iv) It will be seen that here, Dr. Tillyard follows Carpenter in arguing an individual origin of the two suborders Zygoptera and Anisoptera, from a Protozygopterous and Protanisopterous ancestor respectively. It is on this crucial point that I fail to agree with him, since to accept such a theory is to argue that the Nodus, Arculus the Primary pair of antenodal nervures and the nervure *Ac* (*Cuq* of Ris) all had an individual origin. Such a coincidence is beyond credence, as all these are common to and identical in the two suborders. As will be seen later on, Dr. Tillyard states that the nervure *Ac* in *Hemiphlebia mirabilis* is a mere cross-vein, whilst in the whole of the Coenagriidae it is the site of the crossing over of the nervure 1A; the nervure in *Hemiphlebia* is absolutely identical to the rest of the Coenagriidae in structure and position, and the same may be said for it in the whole of the Anisoptera, where it is clearly vestigial in character.—Fraser.

with the posterior margin of the wing, but distinctly separated from it as a fully chitinized main vein, throughout the petiole (v).

There is one other important point to bear in mind concerning the venation of the Odonata. From the very beginning of the Order, apparently through the narrowing of the wings, the two veins MP and CuA, which are of the greatest importance in other Orders, were suppressed. Their basal remnants can be seen in the Meganeuridae (Fig. 5), and the free basal piece of CuA, still extant, is clearly visible in *Kennedya* and *Permolestes*. In all recent forms, not a trace of either of these main veins can be found.

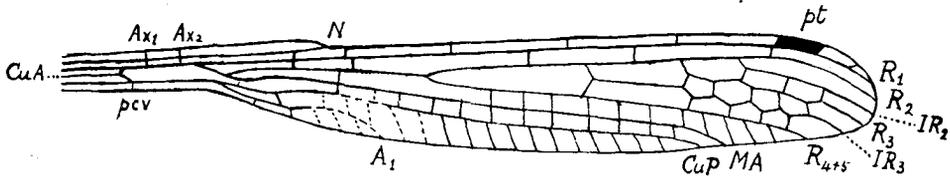


Fig. 6.

Now if we look at the petiole in *Kennedya* (Fig. 9A) and that of *Permolestes* (Fig. 8), we find that the downturned end of CuA, where it falls on to CuP, is supported below by a short cross-vein between CuP and the posterior margin of wing. This is the true *Postcubital cross-vein* (pcv). It might have been imagined that no trace of this cross-vein could be found to exist in any living type. But such is not the case, for if we study carefully the venation of the Platystictidae, we find that this postcubital cross-vein is still in position (Fig. 14) and placed far proximal to the level of the proximal antenodal nervure, while the true anal-crossing (Ac) still forms part of the original subquadrangle. In this remarkable character the family Platystictidae are the most archaic group of Odonata living.

Cross-veins.

The Odonatoid and Plectopteroid Orders differ from the Palaeodictyoptera in not possessing a primitive archedietyon of weakly chitinized

(v) I have examined a considerable number of wings of *Hemiphlebia mirabilis* Selys, to check this statement and find that the anal vein existing as a separate entity as far as the base of the wing is by no means constant. In text-figure 13 I show the various conditions of this vein as existing, not only in different specimens, but even in the wings of individual specimens. Morton was the first to call attention to this peculiarity in the wing of *Hemiphlebia*, which had been pointed out to him by the late Dr. Ris and described by the latter as "A minute cross-vein detached from the anal margin just at the Cuq". Morton states that it does not appear to be constantly present and that Tillyard's figure truly represents the condition of an example in his collection. It should be added that this figure does not show any evidence of a separated anal vein. In the specimens examined by myself, it exists as a separate entity to near the base of wing in one wing only.—Fraser.

polygonal cells. Instead, their cross-vein system is chiefly made up of single cross-veins, strongly chitinized and placed more or less at right angles to the main veins which they connect. Only in special areas of the wing, where a larger space than usual is left between branches of main veins, are polygonal cells developed.

The fossil history of the Odonata shows that the earliest types possessed relatively few cross-veins. The Kennedyidae (Fig. 6) and Hemiphlebiidae (Fig. 12) possess the lowest number. An abundance of cross-veins is to be regarded as a specialization by addition.

Having now indicated the principal specializations in the Odonatoid form of wing-venation, we may proceed to the working out of a new scheme of classification for the Odonatoid Orders of Insects (vi).

Twenty years ago, it would have appeared that the main lines of the Classification of the Order Odonata or Dragonflies were already satisfactorily fixed and that but little remained to be effected in the way of major alterations or improvements. It was true, of course, that comparatively little was known about the actual evolution of the Order. The geological record was at that time a very broken one and consisted mainly of three separate groups, viz.: (1) the gigantic Meganeuridae of the Upper Carboniferous, which were not recognized as true Odonata, but were relegated to the older and long extinct Order Protodonata; (2) the complex of forms found in the European Lias, many of which were recognized as belonging to the Suborder Anisozygoptera; and (3) a number of interesting Tertiary genera, which were admittedly too closely allied to recent forms to be of much value in the study of the evolution of the Order.

(vi) In working out the phylogeny of the Order Odonata, it is very necessary to compare the wing of an archaic form such as *Kennedyia mirabilis* Tillyard, with examples of those belonging to the various families composing the Order, so that one may note the various tendencies which evolution has exhibited in the building up of the wings. These tendencies may be briefly catalogued in chronological order as follows:—1.—A gradual shortening of the subcostal nervure. 2.—The alignment of the two primary antenodal nervures. 3.—The formation of the Nodus and so the Costo-antenodal Complex. 4.—The formation of the Arculus. 5.—The formation of the Discoidal cell, first as an open cleft between main nervures, then a closed quadrilateral, and finally, through bisection of the latter, as two unequal triangular cells. 6.—The recession of the Arculus, Discoidal cell and origins of the nervures $R4 + 5$ and $IR3$ towards the base of the wing. 7.—The lengthening of the Costo-antenodal Complex so as to bring the Nodus nearer the centre of the wing, the primary antenodals lagging behind meanwhile and so lying nearer the base of wing. 8.—The appearance of secondary antenodal nervures in the costal and subcostal spaces, the two sets not coinciding at first, but eventually so. When the whole have coincided the primaries become merged in them and disappear. 9.—The broadening of the base of the wings, especially that of the hind and especially in the Anisoptera. 10.—The appearance of cross-nervures in the median or basal space in many genera especially in recent forms. Lastly, it should be grasped that anisoptery, the normal condition in the Anisoptera, is not confined to that Sub-order, but is very marked among the higher forms of the Zygoptera.—Fraser.

It was the discovery of true Odonata in the Lower Permian of Kansas (Tillyard, 1923, 1925 and 1926) that was the actual event which threw the accepted classification into the melting-pot. But such events do not become historical merely by their occurrence; they only take on a historical significance later, when they can be seen in true perspective. Thus it merely fell to my lot to record the occurrence in the Kansas beds of both Meganeuridae and forms that I considered to be true Odonata, allied to the Zygoptera, and for which I proposed the new Subordinal name Protozygoptera. The actual fossil forms placed by me in the new Suborder were *Kennedyia* Till., *Opter* Sell., and *Ditaxineura* Till. The latter, however, was only represented by the apical portion of a wing and when, later on, Carpenter (1931) discovered a complete wing of this interesting-genus, he was easily able to demonstrate that it had no affinity with *Kennedyia* and *Opter*, but belonged to a new Suborder to which he gave the name Protanisoptera, and which he believed with justice to have been ancestral to the Mesozoic Anisozygoptera.

The next stage towards the completion of the evolutionary history of Odonata was the discovery of further Lower Permian forms in Russia (Martynov, 1930). These were two species of the genus *Sushkinia* Mart., allied to *Kennedyia* Till., and placed in the same family Kennedyidae. About the same time, Carpenter (1931) added the new genus *Progoneura* to the Kennedyidae, from the Lower Permian of Kansas, in the same paper in which he demonstrated the true nature of *Ditaxineura*.

In Russia, Martynov (1931) described two more new species from the Lower Permian, belonging to the new genus *Permaeschna*, and placed them in a further new Suborder Protanisoptera, accidentally choosing the same name as Carpenter had employed for the new Suborder which he had erected to contain *Ditaxineura*. (Although both Carpenter's and Martynov's papers were published in the same year, Carpenter's has priority, as it was issued first (February, 1931). The genus *Permaeschna* is still incompletely known, but it appears highly probable that it must fall within the same Suborder as *Ditaxineura*.)

In the following year, Zalessky (1932) described another interesting genus, *Pholidoptilon*, from the Permian of Russia. Unfortunately this author's knowledge of Odonata is restricted, and another new subordinal name, Permodonata, was added to the rapidly growing list on insufficient grounds.

The fascinating story of the Suborder Protanisoptera was brought to a close for the time being, by the discovery of another new type of wing (Tillyard, 1935), *Polytaxineura* Till., in the Upper Permian of Australia. From a comparative study of all the known types within the Suborder, I was then able to show that it contained two very distinct families, viz., the Ditaxineuridae, containing the single genus *Ditaxineura* Till., and the Polytaxineuridae, containing *Polytaxineura*, *Pholidoptilon* and most probably also *Permaeschna* (vii).

On the Zygopteroid side, the Permian record was gradually enriched, firstly by the description of the fine new genus *Permagrion* (Tillyard, 1928) from the Upper Permian of the Falkland Islands, and secondly by an addition to the Lower Permian of Russia, *Permolestes* (Martynov, 1932). Each

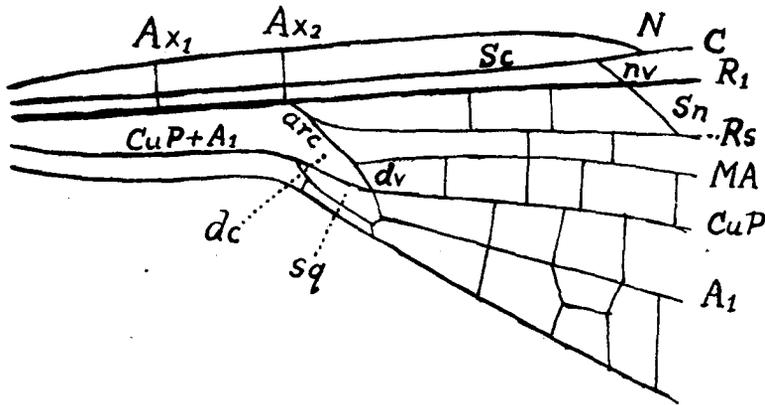


Fig. 7.—*Permagrion falklandicum* Till.

of these fossils possesses complete wings, and each was rightly placed in a separate family. But while *Permolestes* was placed by Martynov within the Suborder Protozygoptera, the Upper Permian *Permagrion* was recognized by myself as being the oldest known member of the Suborder Zygoptera.

Unfortunately the record for the Trias is, up to the present, a poor one. From the Upper Triassic or Rhaetic of Ipswich, Queensland, several forms have been described, but practically all of these are too fragmentary for accurate placing in the scheme of classification. In only one genus, *Triassolestes* Till, is the discoidal cell preserved, and this indicates that the genus stands well inside the true Zygoptera.

I suppose that it would be a truism to assert that, if modern scientists had the complete fossil record of any group ready to their hands, their adopted system of classification would inevitably break down. For all the evolutionary streams in Time are absolutely continuous, and it is only by the elimination of the connecting links that separate species, genera families and orders have arisen. In the case of the Odonata, the interesting position is now arising—indeed it has actually arisen—in which the discovery of annectent fossil forms has obliterated to a large extent the clear-cut distinctions of yesterday, and the question remains—What procedure are we to adopt in the face of such facts?

Two problems have to be faced. The first is—"How are we to deal with the annectent forms themselves in any scheme of classification?" The second is—"How are we to make the major divisions in the whole Odonatoid Complex conform more closely to the new evidence now available?"

The first problem I propose to solve in what appears to me to be the only possible way. Annectent forms should be clearly marked as such, but each should be placed at the end or beginning of that group to which it shows, on a careful analysis, the most marked affinity, with a definite indication also of the group to which, when so placed, it is annectent.

The second problem is the real justification for the present paper,

since it becomes more and more evident, as the discoveries in fossil Odonatoid types multiply, that the present classification is seriously in need of revision, if it is to prove a useful and correct guide to students of the group.

As a starting point for the new classification, I desire here to introduce a remark made by my good friend, Professor A. Martynov. In 1932 (Martynov, 1932, p. 17) he wrote concerning my new interpretation of the wing-venation of the Meganeuridae—"Tillyard proposed (1925, 1928) a quite different interpretation. According to it, the wing-venation in Meganeuridae proved to differ from that in the Protagriidae more strongly than one could think earlier, and I cannot understand why Tillyard has preserved both these same families in the same order".

Martynov then goes on to propose a separate order for the family Meganeuridae, naming it the Order Meganisoptera.

My reply to Martynov is that it was exactly because I desired to avoid this unnecessary multiplication of new Orders that I decided to leave the Meganeuridae within the Order Protodonata, *for the time being*. The differences between *Meganeura* and *Protagrion* were quite as clear to me as they were to Martynov, but I realized that it would require a little of that historical perspective of which I spoke about earlier in this paper, to enable anyone to make a wise use of these differences in readjusting the classification, and therefore I was content to leave the question of reclassification out of my paper. After an interval of more than ten years since my first paper on the Lower Permian Odonata was published, I now think that the necessary historical perspective has been attained, and certainly the available evidence from recorded fossils is very much greater. It is now quite evident to me, and might, I think, have been evident to Martynov in 1932, that a *new Order is not required for the family Meganeuridae*. The completion of the fossil record now gives us a long, single series of forms, in which the evolution of the *nodus* is shown with almost startling clarity, beginning with the normal, simple, elongated subcosta (Meganeuridae), (Fig. 4), and passing on to the Protanisoptera, where the subcosta begins to regress towards the base of the wing and also shows the first sign of nodal formation at its apex, through the specialization of a neighbouring cross-vein into a more or less oblique vein (the nodal veinlet, *nv*), which is destined to link up with $R_{iv} + v$ by means of an intermediate cross-vein, the subnodus (*sn*) lying between R_1 and R_s . We can say, of the Meganeuridae, that none of them possessed a true nodus. Of the Protanisoptera, on the other hand, we can say, with equal truth, that nodal formation has begun, though it is in a far more primitive stage in the Lower Permian *Ditaxineura*, for example, than it is in the Upper Permian *Polytaxineura* or *Pholidoptilon*. Another line of evolution of the nodus is shown in the Protozygoptera where the distal end of the subcosta becomes greatly regressed towards the base of the wing (Kennedyidae) long before the first signs of true nodal formation become apparent.

Reviewing the whole series in perspective, it now appears to me that nothing can be gained by any attempt to make a clear-cut division anywhere in the series of nodal forms. The series is already far too complete for such a division to possess any real value; we may readily grant that the position will become worse with the discovery of each new Palaeozoic fossil form.

Thus one of the main characters which at present separate the Order Protodonata from the Order Odonata is no longer of value.

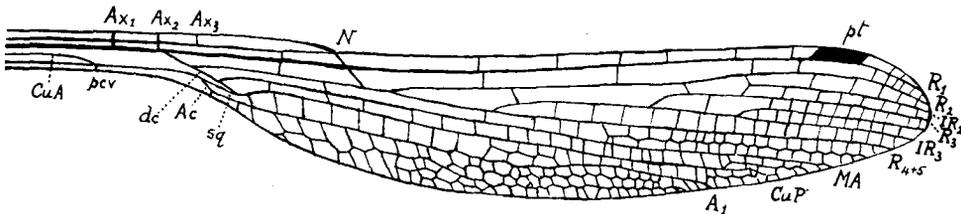


Fig. 8.

A second evolutionary line is exhibited in almost as complete a fashion, in the formation of the *discoidal cell*. It begins in the strong sigmoidal waving of CuP and 1A in the Meganeuridae (Fig. 4) and is continued into the Ditaxineuridae and Kennedyidae with only a single important difference, viz., that the number of cross-veins is very greatly diminished. In none of these forms is a true discoidal cell developed, but it is possible in both Ditaxineuridae and Kennedyidae to indicate that particular cross-vein (the discoidal cross-vein, *dv*) which, later on, is destined to form the distal side of the quadrangle (discoidal cell). The "open discoidal cell" of such types as *Permagrion*, *Permolestes*, *Hemiphlebia* (forewing only) and *Chorismagrion* (forewing only), is formed merely by a change in the character of this cross-vein *dv*, which begins as a short cross-vein, more or less at right-angles to the main veins which it connects, and develops into an oblique vein continuing the course of the arculus downwards.

It will be abundantly clear, therefore, that if we desire to retain the Meganeuridae within the Protodonata on the ground that these forms possessed no true nodus, then it would be very difficult to omit some of the Lower Permian forms placed in the Protozgyoptera and Protanisoptera especially *Kennedy*. If, on the other hand, we desire to retain the Meganeuridae within the Protodonata because of the absence of a discoidal cell, then it is clear that *Ditaxineura*, *Kennedy* and allies would have to be removed to the Protodonata with them.

Martynov is quite correct of course, when he states (1932, p. 17) that the affinities of the family Meganeuridae are much closer to the Protanisoptera and Anisoptera than they are to the remaining Protodonata.

Here it is necessary to ask ourselves what would be left of the Order Protodonata if we removed the dominant group Meganeuridae from it? The original genus on which the Order was founded by Brongniart (1898) was *Protagrion* Brong. (Fig. 3). This genus, together with two allied genera from the Permian (*Calvertiella* Till., *Tillyardiella* Mart.), differ markedly from the Meganeuridae and all true Odonata, and agree closely with the Palaeodictyoptera in possessing a full complement of original convex and concave veins. In these forms, the concave vein MP and the convex vein CuA remain complete. In the Meganeuridae only small portions, at the base, of both these veins are still preserved. In the Kennedyidae and Ditaxineuridae, MP is completely suppressed, and only

a short basal piece of CuA is retained within the "basilar space" lying between R + M above and CuP below. In all forms of Odonata from the Upper Permian to the present day, as far as they are known (with the sole possible exception of *Tarsophlebiopsis* Till.), both MP and CuA have been completely suppressed.

It thus appears to me that the only possible subdivision which can at present be made between the Protodonata and the Odonata must be based upon a single very important character, viz., the presence or absence of the complete veins MP and CuA, and therefore *the Meganeuridae must from now onwards be regarded as true Odonata!*

With the Meganeuridae removed, the old Order Protodonata becomes a mere remnant of three genera—*Protagrion*, *Calvertiella* and *Tillyardiella*. Following on this, the question at once arises as to whether these remaining forms are really distinct enough from some of the forms placed within the Palaeodictyoptera to warrant the retention of the ordinal name. I think that a decision on this point cannot be made without a very full analysis of the characters of certain families of Palaeodictyoptera and also a very complete study of all forms related to the Order Archodonata of Martynov, which includes only the genus *Palaeothemis* Mart. In particular, it would appear important that we should thoroughly understand the composition of the anal veins in all these forms and their relationship to the anal veins in the Plectopteroid complex, to which they are more or less distinctly allied.

In the present paper, I propose to include as true Odonata all those forms in which the two main veins MP and CuA are either entirely absent or else represented by small basal remnants. Under this system, the family Meganeuridae must take its place as the most primitive types yet known within the Order, and be classified as a Suborder of the Order Odonata, with the name Meganisoptera (= Order Meganisoptera Mart.).

It will, I trust, be fully understood that, as nearly all the fossil forms are known only from the wings, the characters used in defining the various groups which include fossils, must be drawn from the wing-venation. Undoubtedly if we had the fossil evidence preserved, other characters of great importance would be available, e.g. the amount of obliquity of the thorax, the number of tarsal segments, etc. But as matters stand, we must be thankful that the parts of an insect most generally preserved as fossils, viz., the wings and wing-venation, are just those which are of the greatest importance in the recognition of the various orders and families.

The following definitions will now serve to distinguish the Order Protodonata from the Order Odonata:—

Order PROTODONATA (Brongniart, emend. Handlirsch). (Fig. 3).

Palaeopterous insects having wings of Oodonatoid facies but retaining the archaic Palaeodictyopterous character of possessing a complete series of alternating convex and concave veins, including completely formed posterior media (MP), and completely formed anterior cubitus (CuA).

Suborder. 1. ARCHODONATA Martynov. Wings without a system of cross-veins; pterostigma present with the elongate subcosta passing through it; a pseudonodus formed on costa before halfway to apex. Anal system of veins resembling that of the Plectoptera,

with three convex anal veins, A1, A2, and A3, together with an intercalated concave anal vein, 1A, situated between A1 and A2.

Only a single family, Palaeothemidae Mart., with a single genus, *Palaeothemis* Mart. (Upper Permian, Russia).

Suborder 2. PALAEODONATA *nov. nom.* Wings with a complete system of cross-veins; pterostigma absent; subcosta extending well towards apex of wings; no nodal formation. Anal system of veins consisting of a single long convex anal vein, 1A, provided with a posteriorly placed, descending system of branches.

Only a single family, Protagriidae Mart., with three genera, *Protagrion* Brong. (Fig. 3). (Upper Carboniferous, France), *Calvertiella* Till. (Lower Permian, Kansas), and *Tillyardiella* Mart. (Upper Permian, Russia).

Order ODONATA Fabricius.

Palaeopterous insects in which the archaic Palaeodictyopterous characters of the wings are modified by the suppression of two of the main veins, viz., the concave posterior media, (MP), and the convex anterior cubitus, (CuA), which are usually entirely absent, though short basal remnants of one or both of these veins can still be found in a few of the older fossil forms. Anal system of veins consisting always of a single convex first anal (1A), which, in some narrow-winged or petiolate forms, is fused basally with CuP, or may even, in extreme cases (Archizyoptera) be entirely suppressed.

Key to the Suborders of the Order ODONATA.

1. Primitive forms with very narrow wings, petiolate or subpetiolate, having a short subcosta ending well before half-way to apex; no true nodus or discoidal cell 2.
Not such forms 3.
2. Two or three antenodals present; postnodals few in number; a basal remnant of CuA present; subdiscoidal cell present; pterostigma present; number of cross-veins comparatively small PROTOZYOPTERA Till.
Antenodals absent; postnodals numerous; subcosta excessively short; no basal remnant of CuA present; no subdiscoidal cell; pterostigma present; number of cross-veins comparatively large. ARCHIZYOPTERA Handl.
3. Large to very large Palaeozoic forms with the subcosta well developed, reaching from about half-way to near apex of wing; no true nodal formation; pterostigma absent; basal remnants of MP and CuA present or absent; CuP and 1A both sigmoidally waved in basal halves; no discoidal or subdiscoidal cell present. MEGANISOPTERA Mart.
Not such forms. Pterostigma present in all save a few very highly specialized types (in which it becomes obsolete); sub-

costa never extending beyond two-thirds of the costa; nodus either completely or partly formed; either a discoidal or subdiscoidal cell always present 4.

4. Primitive Palaeozoic (possibly also Mesozoic) types with the subcosta ending more than half-way along the costa; nodal formation incomplete or complete; pterostigma present, extending well below R₁; CuP and 1A both strongly arched upwards in region of arcus; no true discoidal cell present but a subdiscoidal cell always defined PROTANISOPTERA Carp.

Not such forms. Discoidal cell always present although in the more primitive forms it may be open basally in both wings or forewing only 5.

5. Wings never petiolate; in both fore and hind wings the discoidal cell is subdivided into a triangle plus supratriangle. ANISOPTERA auct.

Wings petiolate, subpetiolate or non-petiolate; discoidal cell either undivided, or, if divided into triangle plus supratriangle, then this formation is confined to the hind wing 6.

6. Discoidal cell of both wings simple, entire or traversed by nervures closely similar in fore and hind wings ZYGOPTERA auct.

Discoidal cell differing in form in fore and hind wings; in the hind wing it may be either a single cell or divided into triangle plus supratriangle ANISOZYGOPTERA Handl.

Suborder I. MEGANISOPTERA Mart. (Figs. 4, 5).

Order *Meganisoptera* Mart., 1932, Trav. Inst. Palaeozool. Acad. Sci. URSS, 1:1-44, pl. i. (p. 17).

Handlirsch recognized two families, the Meganeuridae and Paralogidae, distinguished by the shape of the wing and the separation or union of the basal stems of R₁ and R_s + MA. The discovery of a considerable number of intermediate forms since Handlirsch wrote has almost bridged the gap between his two families. I therefore propose to recognize only the one family Meganeuridae, with the following genera:—

Upper Carboniferous:—

European genera:—*Meganeura* Brong., *Meganeurella* Handl., *Meganeurina* Handl., *Meganeurites* Handl., *Boltonites* Handl., *Truemanina* Bolton, *Ephemerites* Geinitz, *Gilsonia* Meunier.

North American genera:—*Palaeotherates* Handl., *Paralogus* Scudd., *Paralogopsis* Handl.

Permian:—

European genera:—*Arctotypus* Mart.

North American genera:—*Typus* Sell., *Megatypus* Till., *Oligotypus* Carp.

Mesozoic genera doubtfully belonging to this Suborder:—*Reisia* Handl., *Piroutetia* Meunier, *Schlectendaliola* Handl. ? (larval).

Suborder 2. PROTOZYGOPTERA Till. (Figs. 6, 8).

Protozygoptera Tillyard, 1925, Amer. J. Sci., 10 (55): 41-73. (p. 62).

This Suborder begins the very distinct series of forms which may be classified together under the term "Zygopteroid Complex". The earliest types are small forms with extremely narrow wings, having marked petiolation. The subcosta is always greatly shortened and never, even in the most highly specialized types within the Complex, reaches as far as half-way along the wing. The pterostigma is well formed in the oldest known types, being a narrow, elongate rectangle in form and not extending below R₁; in the more highly evolved types within the Complex, many different types of pterostigma arise, and in one evolutionary line the pterostigma becomes at first obsolescent and then obsolete in a few genera. Nodal for-

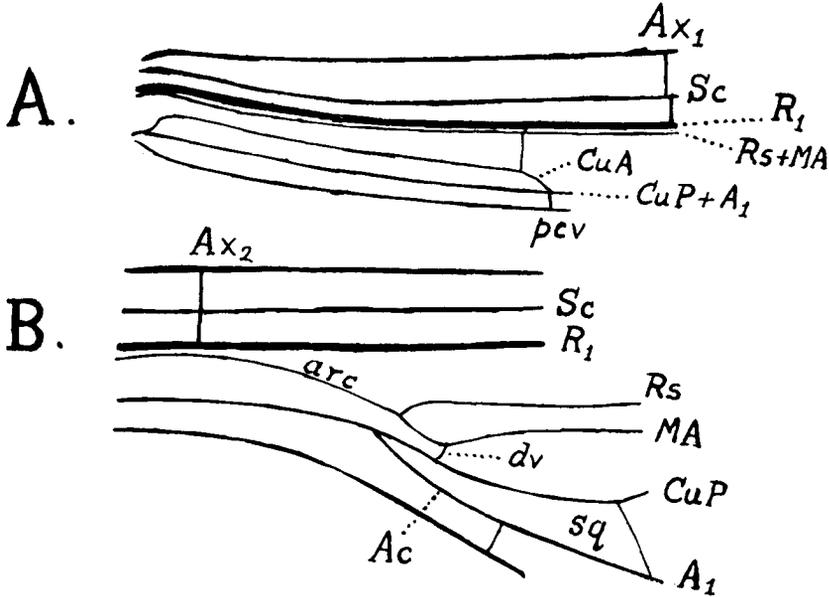


Fig. 9.

mation begins with a slight bend of the costa at end of Sc, followed by fixation of a cross-vein below this point and later by the addition of a subnodus, but there is no fixation of Riv + v below the subnodus as in the Anisopteroid Complex. The earliest types, probably in correlation with the petiolation of the wings, have CuP fused with 1A basally. The original sigmoidal arching of CuP, inherited from a common ancestor with the Meganisoptera, is retained in the region of the arculus, but at first there is no true discoidal cell present, only a single cross-vein situated between the downwardly bending portions of MA and CuP. This cross-vein (*dv*) later becomes oblique and forms the distal side of the discoidal cell or quadrilateral. A subdiscoidal cell (*sdc*) is present in the oldest forms, lying between the diverging veins CuP and 1A where they separate; this cell undergoes many vicissitudes in the higher forms. Generally speaking, the oldest forms possess the smallest number of cross-veins, with only two or at most three antenodals and very few postnodals. Two tendencies

operate on the cross-vein system in the course of evolution: the first, leading to the Coenagrionidae, tends to arrange the existing cross-veins into transverse series; the second, leading to the Agriionidae, tends to increase the number of cross-veins greatly.

The Zygopteroid Complex, after throwing off an unsuccessful side-branch, the Archizygoptera, in early Mesozoic times, ran out into the highly successful Suborder Zygoptera as we know it to-day.

The principal characters of the wings of the Protozygoptera may be simply stated as follows:—

Wings very narrow, petiolate; usually only two, more rarely three antenodals; very few postnodals. Sc short, ending well before half-way to apex of wing. Nodus incomplete, merely a more or less marked indentation of the costa where Sc joins it, and with or without a nodal veinlet beneath it. Pterostigma well formed, strongly chitinized, narrow, elongate, rectangular in shape. A short but definitely convex basal remnant of CuA present in the basilar space, extending for less than half the length of the petiole. R and MA completely fused together basally; arculus formed by a downward divergence of Rs + MA from R1; shortly after it, Rs and MA again diverge and then run subparallel to one another. Rs is a concave vein with pectinate descending posterior branches, altogether five in number, of which three are concave original branches of Rs, viz., R2, R3, and R4 + 5, while two are intercalated convex veins, viz., 1R2 and 1R3. MA and CuP both end up on the posterior margin well beyond half-way to apex of wing but 1A may be either long or short.

Two families are represented, which may be distinguished as follows:—

- No nodal veinlet aligned below end of SC; cross-veins few in all parts of the wing; 1A short KENNEDYIDAE Till.
 A nodal veinlet aligned obliquely below end of SC; cross-veins numerous in posterior part of wing; 1A moderately long PERMOLESTIDAE Mart.

The following genera are known:—

- Family KENNEDYIDAE:—Lower Permian of Kansas—*Kennedy* Till,
Progoneura Carp., *Opter* Sell.
 Family PERMOLESTIDAE:—Lower Permian of Russia—*Permolestes*
 Mart.

ANNEXENT FORM:—The genus *Permolestes* Mart., might with almost equal justice be classified within the Zygoptera, but the presence of the short basal piece of CuA makes it more advisable to retain it within the Protozygoptera. It is well advanced beyond the stage shown in Kennedyidae, in the higher development of the nodus, the great increase in the development of the cross-vein system in all posterior parts of the wing, and in the longer and much more specialized 1A. In general appearance, the wing of *Permolestes* reminds one quite strongly of the Lestidae, but actually it serves in many ways to connect the Kennedyidae with the first known genus of true Zygoptera, viz.—*Permagrion* Till. (Upper Permian of the Falkland Islands) (Figs. 7, 8).

Suborder 3. ARCHIZYGOPTERA Handl. (Fig. 10.).

Archi-Zygoptera Handlirsch, 1908, Die Fossilen Insekten: 471.

(The name *Archi-Zygoptera* has here been altered to conform with the Rules.)

The Archizygoptera are a little known group of very curious forms which were evidently evolved from early types of Protozygoptera during the early part of the Mesozoic through further reduction of the veins Sc and 1A together with a large increase of the number of cross-veins distal to Sc, and the evolution of a highly specialized arrangement of the branches of

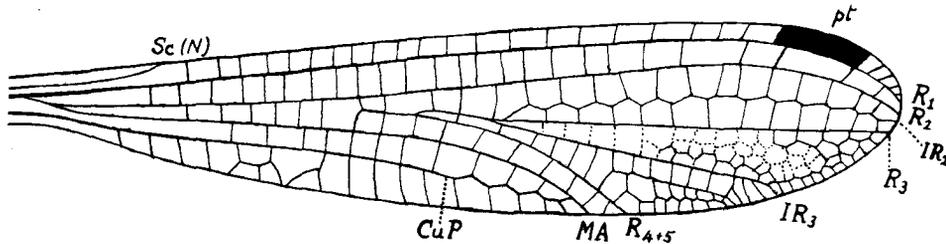


Fig. 10.

Rs. Unfortunately the wings are extremely delicate, so that, although a number of specimens are known from the Trias, Lias and Jurassic, it is still impossible to interpret the venation with absolute certainty.

The characters of the Suborder are as follows:—

Wings narrow, petiolate or subpetiolate. Sc reduced to a mere remnant, reaching less than one-fifth of the wing length along costa. No antenodals present, but numerous postnodals in the long space between the end of Sc and the rectangular pterostigma. Cross-veins abundant in all parts of the wing except near the base. No true nodus, and apparently, not even an indentation of the costa at the end of Sc. No sign of a discoidal cell or subdiscoidal cell and no discoidal cross-vein. The branches of Rs are very specialized, the intercalated veins 1R2 and 1R3 taking the form of straight intercalated sectors, and all the branches diverging from one another at extremely acute angles; between these branches, a polygonal mesh-work of cellules is beginning to form. A very marked character is the manner in which the two primary branches of Rs separate from one another; they diverge at an acute angle and then R4 + 5 arches strongly downwards so as to be curved concavely to the posterior margin throughout its length. At the same time, the apical portion of the wing is strengthened by the long intercalated vein 1R2 taking on the form of an absolutely straight vein running longitudinally through the wing and apparently joining R3 basally, while the latter vein also becomes a strong, straight vein running obliquely to well below the apex. 1R3 is a short, straight intercalated vein lying just below and parallel to R3. MA and CuP are well formed veins extending, as in Protozygoptera, well beyond half-way along the posterior margin of wing; but 1A appears to be either completely lost, or only represented by a short series of zigzagged veinlets below CuP.

There is only one family, the Protomyrmeleontidae, containing the following genera:—

Triassic (Australia):—*Triassagrion* Till.

Liassic to Jurassic (Europe and Asia):—*Protomyrmeleon* Geinitz, *Tillyardagrion* Mart.

Suborder 4. ZYGOPTERA auct. (Figs. 11, 12, 15-27.).

In this immense Suborder, beginning in the Upper Permian and extending to the present day are included all those types of damsel-flies in which a definite *discoidal cell* is formed below the arculus. For purposes of

classification, this cell may be either *open* or *closed* basally, that is to say, the formation of the cell is reckoned not from the time that it becomes closed-in basally by the provision of an extra cross-vein to form its basal side, but from the time when, through the oblique alignment of the original discoidal cross-vein (*dv*) with the basal free piece of *Rs* and *MA* above it, a complete *arculus formation* is provided connecting *R* with *CuP*. The *discoidal cell* or *quadrangle* (*q*) is then defined as the space between the oblique basal portion of *MA* above and the curving portion of *CuP* below; its distal side, *dv*, tends in the oldest types to extend the line of the basal portion of *MA*, but later on takes on greater individuality, when the discoidal cell becomes closed basally by an extra cross-vein.

That this is the only logical way to consider the discoidal cell must be evident when we study primitive living forms as *Hemiphlebia* and *Choris-magrion*, in which the two stages of evolution of this cell are exhibited in a single insect. In the forewings of these two genera, the discoidal cell remains open and keeps the primitive form found in the Permian genus *Permagrion* Till., but in the hind wings, the same cell is closed and forms a typical quadrilateral.

It should be noted that, as only a single wing of the Permian age is known, it cannot be stated definitely that this form possessed open discoidal cells in both fore and hind wings. It is indeed quite possible that this Permian wing represents a fore wing. At any rate, until more is known about it, the Permian genus cannot be given anything more than family rank within the Suborder Zygoptera.

Amongst the immense number of genera belonging to the Zygoptera, the venational characters are so diverse that a definition of the Suborder must rest mainly on the structure of the discoidal cell, other characters taking only secondary place. The Suborder may then be defined as follows:—

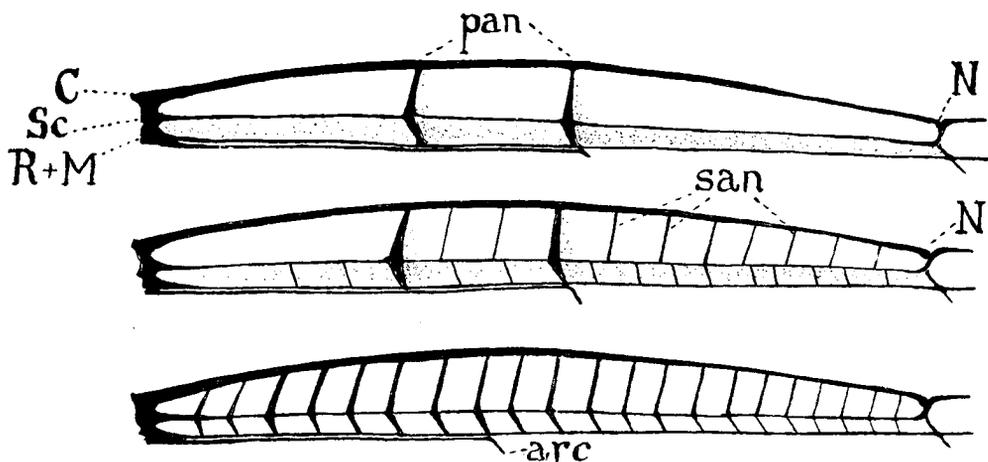


Fig. 11.

More or less delicately built dragonflies (damselflies) with fore and hind wings closely similar in size, shape and venation, slender to moderately wide wings, petiolate, subpetiolate or non-petiolate, but never greatly

widened near base. Sc always ending before half-way along costa. Nodus always partly or wholly formed, the most primitive type (Permian) having a marked indentation of the costa at end of Sc, with an imperfect alignment of the nodal veinlet (*nv*) and subnodus (*sn*) below it; in all higher types, the nodus is complete. Antenodals originally only two or three, but becoming numerous in higher types. Postnodals originally very few, but increasing in number in higher types. Pterostigma originally rhomboidal or rectangular, but varying greatly in form in the higher types; in a few genera, it may even be obsolete. Rs with three primary (concave) and two intercalated (convex) branches, as in the Protozygoptera, but many additional intercalated sectors may be present in some of the higher forms. Discoidal cell or quadrilateral similar in fore and hindwings, open basally in a few primitive forms only (in forewings only of two genera, *Hemiphlebia* and *Chorismagrion*); this cell may be simple or crossed, but is never subdivided into triangle plus supra-triangle as in the Anisoptera or hindwings of some Anisozygoptera. CuP and 1A of variable length; in some forms, both these veins are shortened, and 1A may even be entirely suppressed (as in Archizygoptera).

With the discovery of new types, including a Permian and some incomplete Triassic genera, the task of tracing out the evolutionary line within the Zygoptera is becoming a very formidable one. Nevertheless, it is now clear that it would have been quite impossible to offer a phylogenetically accurate classification of the Suborder without the knowledge of these new genera, even though we may well suspect that, with our present knowledge, any classification that may be offered, will be sure to undergo further changes.

The classical method of subdividing the Zygoptera is into two groups (originally families, in the Selysian sense), according to the number of antenodals present. In the Superfamily Coenagriioidea (family Agriioidea of Selys et auct.) there are usually only two antenodals, very rarely from three to five. Any additional or secondary antenodals are incomplete and found only in the costal space. In the Superfamily Agriioidea (family Calopterygidae of Selys et auct.) the antenodals are numerous, the lowest number being five, and there are always more than two which occupy both costal and subcostal spaces.

It will be seen that, if this classification were to be accepted, the Permian genus *Permagrion* Till., would fall within the Coenagriidae, as would also the genera *Hemiphlebia* and *Chorismagrion* in both of which the discoidal cell of the forewing is open basally.

Admittedly these three genera are all very archaic. But, in my opinion, *Hemiphlebia* is the most archaic of the three, for the following reasons:—

(1) The second (distal) antenodal stands well before the level of the arculus. This agrees with the condition found in the Protozygoptera. In all other true Zygoptera possessing two antenodals, even including *Permagrion*, the second antenodal is either directly above the origin of the arculus or extremely close to it (vii).

(vii) This statement is not quite correct, since in several genera of the Coenagriidae, the arculus stands well distal to the level of the distal primary antenodal, viz., *Agriocnemis*, *Argiocnemis*, etc. In some species of *Cephalaeschna* the arculus also occupies a position comparable to that found in *Hemiphlebia*.—Fraser.

(2) Only occasionally do the postnodals in *Hemiphlebia* line up with those cross-veins in the space immediately adjoining them. In this character, *Hemiphlebia* agrees with the Agrioidea, but disagrees with all other Coenagriodea, inclusive of *Permagrion*.

(3) The posterior margin of the wing in *Hemiphlebia* if followed back beyond the anal crossing (Ac) towards the base, can be seen to be composed of two contiguous but distinct veins, viz., the true anal vein, 1A, placed anteriorly, and the posterior margin, which resembles the costa in being armed with distinct serrations, though these are weaker and placed more widely apart than on the costa. In this character also the genus *Hemiphlebia* resembles the Agrioidea and differs from all other Coenagriodea, including even *Permagrion* (not to mention also the Protozygoptera), in which the posterior margin of the wing up to the anal crossing is a simple chitinization. (See footnote (v) and text-fig. 13.)

I had previously (1926) explained this important character by supposing that a secondary anal vein was in process of formation backwards towards the base of wing from Ac, and that *Hemiphlebia* exhibited the first stage of this formation. This explanation follows immediately on the acceptance of the precedent tracheation as a guide to the subsequent venation. But I am now inclined to agree with Carpenter (1931, p. 112) that the tracheation may be as unreliable in this case as I had previously shown it to be in the case of the supposed crossing-over of Rs in the Anisoptera. In that case, *Hemiphlebia* is again seen to stand at the very base of the Agrioidea rather than of the Coenagriodea (viii).

(4) The discovery of the larva of *Hemiphlebia* (Tillyard, 1928) shows that it is a far more primitive type than any other known larva.

I therefore propose to separate *Hemiphlebia* out, not merely as a distinct family, as I did in 1926, but as a superfamily of its own standing at the very base of the whole Suborder, and combining certain characters of both the other two superfamilies. It agrees with the Coenagriodea in possessing only two antenodals and generally in the simplicity of its venation, but it also agrees with the Agrioidea in having no alignment of the postnodals with those cross-nervures in the adjacent space posteriorly, and also in the presence of the anal vein, distinct from the posterior margin basally from the anal crossing, Ac.

The following key will now separate out the three superfamilies into which I propose to subdivide the Zygoptera:—

1. Distance from base of wing to arculus either greater than distance from arculus to nodus, or, at the least, equal to it. Antenodals normally two only, rarely from three to five, in which case the additional ones are incomplete (except in *Neurolestes*, which has three complete antenodals). Discoidal cell entire (crossed only in *Anomisma*), always a closed quadrilateral except in some early fossil

(viii) I am not inclined to share Dr. Tillyard's or Professor Carpenter's opinion in this, since it still leaves us with the nervure Ac to account for. This is present in *Hemiphlebia* and can be followed right through the whole Order, occupying the same position. If only a simple cross-nervure, surely we should expect to find some variation in its position? Its constancy stamps it as a vestigial structure and no other explanation but that it is the site of the crossing-over of the nervure 1A will meet the case. In Part II. of this paper, I shall endeavour to show by means of diagrams that Dr. Tillyard's first supposition was the correct one.—Fraser.

- forms and in the forewings of *Hemiphlebia* and *Chorismagrion*, where it is open basally 2.
 Distance from base of wing to arculus always less than distance from arculus to nodus, usually much less (in *Disparocypha* only slightly less). Antenodals always more than two, never less than five; discoidal cell nearly always crossed (entire only in *Disparocypha*, *Philoganga*, *Amphipteryx* and *Diphlebia*), never open basally Superfamily AGRIOIDEA Till.
2. Postnodals of first and second series not aligned with one another. Anal vein visible as a separate vein from base of wing outwards, contiguous with the posterior margin up to Ac Superfamily HEMIPHLEBIOIDEA Till.
 Postnodals of first and second series aligned with one another, either wholly or in part. No sign of a separate vein from base of wing to Ac Superfamily COENAGRIOIDEA Till.

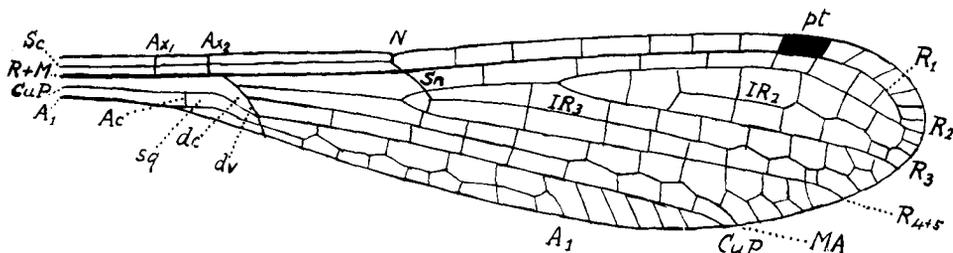


Fig. 12.

Superfamily HEMIPHLEBIOIDEA Tillyard. (Figs. 12, 13.)

Antenodals two in number only, of which the distal one is situated proximal to the level of the arculus; no alignment of any postnodals with cross-nerve posterior to themselves; discoidal cell of forewing open, that of hindwing closed; subdiscoidal cell fully formed; anal vein partly fused with posterior margin of wing basally, but separating from it just before the anal crossing (Ac) which forms the basal side of the subquadrate.

Family HEMIPHLEBIDAE Tillyard.

There is only one family, the Hemiphlebiidae, containing a single genus, *Hemiphlebia* Selys, with a single species, *H. mirabilis* Selys, confined, so far as is at present known, to a single habitat on the Goulburn River, near Alexandra Victoria, Australia (ix).

(ix) The types of this species are stated by Selys to have come from Port Denison, Queensland (received from M. Weyers), and the same locality is given for types of *Synlestes weyersi* Selys. Having recently visited Bowen (Port Denison), North Queensland and explored the country all round it, I can say with certainty that neither of these two species can possibly have occurred anywhere in that region; firstly because there is no suitable type of fresh-water for their larvae to exist in, and, secondly, because the region is a dry one, subject to prolonged drought almost yearly. The species *Synlestes weyersi* is abundant in suitable localities in Victoria, New South Wales and South Queensland, but has not been taken further north than

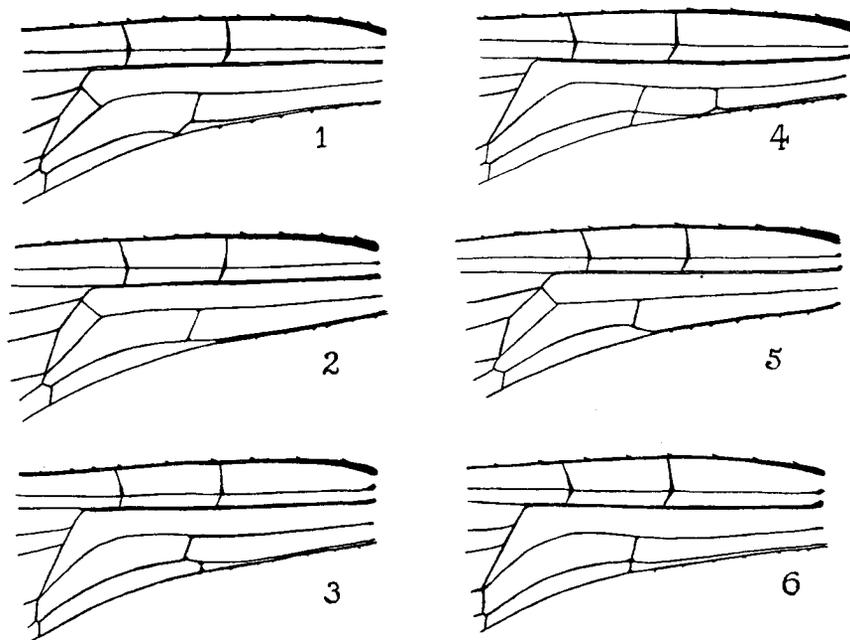


Fig. 13.

To the superfamily characters may be added the following as of only family or generic value:—

Size very small; abdomen very slender, extending beyond the wings; petiolation of wings not clearly marked off by an indentation or angulation of posterior margin of wing; postnodals 5-6 in number, only normally 4 in the space posterior to them; pterostigma short, rhomboidal, covering a single cell; veins 1R2 and 1R3, together with some distal cross-veins, distinctly hairy. In forewing, there is a single oblique line formed between R and 1A by the following elements—(a) upper portion of arculus, (b) distal side of the open discoidal cell, (c) short distal side of subdiscoidal cell. In both wings, the anal-crossing, (Ac) is to be interpreted as a mere cross-vein impinging upon the vein 1A just after it leaves the posterior margin. A study of the tracheation of the nymphal wing indicates that at no time is any trachea present, and therefore this cross-vein cannot very well represent the previous crossing-over of such a trachea from the line of CuP to the posterior margin. It might, however, be interpreted as the homologue of the cross-vein which, in *Kennedya* and *Permolestes*, supports the downturned end of the primitive basal remnant of CuA from below.

For a full understanding of the importance of the genus *Hemiphlebia*

the Blackall Ranges, approximately 100 miles north of Brisbane. I have searched very large areas of suitable country in Eastern Australia for *Hemiphlebia* without success, except for the original locality discovered many years ago by Captain Billinghamurst and recorded by Rene Martin (1904).—Tillyard.

in any scheme of classification of the Zygoptera, it would be necessary to give a much more complete account of the insect, enumerating not only its venational peculiarities, but also the many archaic characters to be found in its head, thorax, abdomen and anal appendages, in the remarkably archaic larva or nymph and in the tracheation of the nymphal wings. These however, are outside the scope of the present paper.

Superfamily 2. COENAGRIODEA Tillyard (emend.) (Figs. 14-27.).

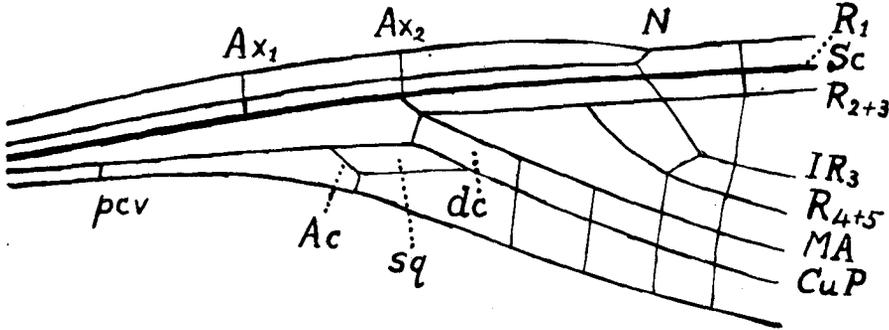


Fig. 14.

Antenodals only two in number, very rarely three, four or five, in which cases the additional ones are found only in the costal space; distal antenodal situated directly above and in line with the arculus or the arculus situated slightly distal to it; postnodals usually corresponding with the cross-nervures in the space posterior to themselves, except for the distal one or two; at the least, the more proximal postnodals are aligned, though the distal ones may not be (e.g., *Argia*). Pterostigma variable in form, always present and in some cases hypertrophied. Discoidal cell (dc or q) complete in every case except only in the forewing of genus *Chorismagrion* (Synlestidae) and in the only known wing of the Permian genus *Permagrion*, which may also be a forewing. Originally all the branches of Rs arose distal to the nodus, as in *Permagrion*; in the course of evolution, the origins of these branches have tended to move basally, until, at the present day, only a few primitive genera retain this condition; in the great majority of forms, either the origin of R4 + 5 is in line with the subnodus, or that of IR3 is in line with it and that of R4 + 5 is slightly proximal to it, or both these veins have moved well proximal to the level of the subnodus. The subdiscoidal cell either completely formed, not touching the posterior margin, or meeting it at a point, or completely eliminated. Veins CuP and 1A either both long and complete, or one or both of them reduced or completely eliminated. Additional intercalated sectors sometimes present; in extreme cases, these occur distally between all main veins from R1 to 1A.

The following key will serve to distinguish the known families of the Coenagriodea:—

1. Discoidal cell open basally; nodal vein (*nv*) and subnodus (*sn*) situated in an oblique line markedly before the level of Sc, that is Sc extends distal to the line of *nv* PERMAGRIIDAE Till.
Discoidal cell closed basally (except in the forewing of *Chorismagrion*); nodal vein and subnodus in an oblique line situated at the level of the distal end of Sc. 2.

2. CuP arching strongly upwards on leaving the discoidal cell SYNLESTIDAE Till.
CuP not arched strongly at this point 3.
3. R4 + 5 and 1R3 both arising far proximal to the level of subnodus, 1R3 usually at least half-way between arculus and subnodus and usually nearer the arculus 4.
R4 + 5 and 1R3 arising nearer the subnodus than arculus; at the most, R4 + 5 arising half-way between arculus and subnodus 5.
4. Veins CuP and 1A complete; supplementary sectors present between 1R3, R4 + 5 and MA LESTIDAE auct.
Vein CuP greatly reduced, vein 1A entirely absent; two straight supplementary sectors present, one between R2 and 1R2 and another between 1R2 and R3 LESTOIDEIDAE Till.
5. Nodus situated very close to base of wing, at from one-sixth to one-fourth the wing-length; pterostigma absent, or if present, abnormal, not fully chitinized, or made up of several cells, never braced PSEUDOSTIGMATIDAE auct.
Nodus lying more distal, usually more than one-fourth the wing-length from base (if nearer, then the pterostigma normal); pterostigma present, strongly chitinized (rarely hypertrophied), braced or unbraced 6.
6. Supplementary sectors present distally and extending proximal as far as the level of pterostigma or further MEGAPODAGRIDAE Till.
Supplementary sectors absent or at most a few distal cellules aligned and not extending proximal as far as pterostigma 7.
7. Vein 1A absent or greatly reduced; vein CuP normal or reduced 8.
Veins CuP and 1A normal 9.
8. An extra cross-vein present in the postcostal space, very close to base of wing and in addition to that of the anal-crossing (Ac); number of postnodals comparatively large PLATYSTICTIDAE Fraser.
No additional cross-vein in the postcostal space; number of postnodals comparatively small PROTONEURIDAE Till.
9. Discoidal cell subrectangular; no marked zig-zagging of any of the main veins (only distal portion of MA slightly zig-zagged) PLATYCNEMIDIDAE Till.
Discoidal cell with distal angle markedly acute; veins 1R3, MA and 1A strongly zig-zagged distally COENAGRIDAE Till.

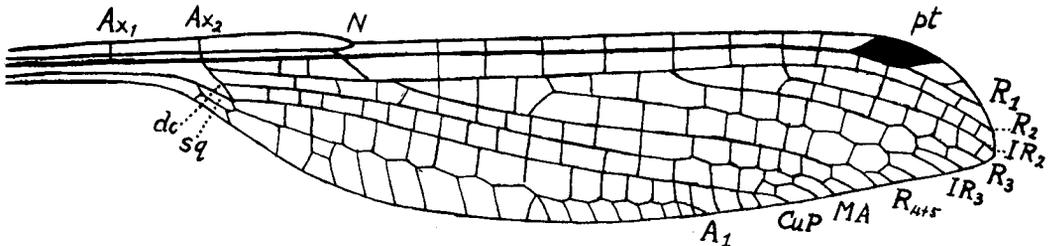


Fig. 15.

Family I. PERMAGRIIDAE Tillyard. (Figs. 7, 15.).

Permagriidae Till., 1928, Trans. Roy. Ent. Soc. Lond., 1: 56.

The single wing from the Upper Permian of the Falkland Islands forms a connecting link between the Lower Permian Kennedyidae (Suborder Protozygoptera) and recent Zygoptera. Though *Permagrion falklandicum* is probably not ancestral to any existing form, it obviously lies fairly close to the ancestors of the Synlestidae, especially *Chorismagrion*. From all known Zygoptera of later geological dates, it differs in the less complete formation of the nodus, in which the nodal vein and subnodus have not yet become as closely aligned with the tip of Sc as in other forms. In this and some other respects it stands at nearly the same level as *Permolestes*, but it is well in advance of the latter in the complete loss of the primitive basal remnant of CuA, and must therefore be placed within the true Zygoptera.

Its venational characters are as follows:—Antenodals two in number only, the distal in line with the arculus; postnodals eight in number, all coinciding with the cross-nervures immediately beneath them; apex of wing somewhat falcate; pterostigma rhomboidal, covering two cells; no alignment of cross-veins into transverse rows in distal part of wing below R₂. All branches of Rs arising distal to subnodus; R₄ + 5 arising slightly distal to subnodus, barely one cell's length, the other three branches at nearly equal intervals apart; 1R₃ four cells distal from R₄ + 5; R₃ three cells distal to 1R₃, and 1R₂ two cells distal to R₃; 1R₃, MA and 1A slightly zig-zagged in their distal portions, the other veins straight; discoidal cell open basally, its distal angle acute, its distal side practically in line with the arculus; subdiscoidal cell (sq) completely formed by closure of the first cell between CuP and 1A after they separate, the distal side being formed by a strong oblique cross-vein descending from the distal side of discoidal cell. Only a slight upward arching of CuP after leaving the discoidal cell. The space between the middle of 1A and the posterior margin of wing rather wide.

Only a single genus is known, *Permagrion* Till., from the Upper Permian of the Falkland Islands.

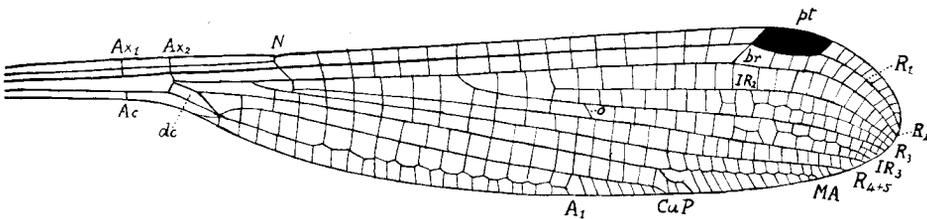


Fig. 16.

Family 2. SYNLESTIDAE Tillyard. (Figs. 16, 17.).

Synlestidae Till., 1926, Insects of Australia and New Zealand, 78.

This family can be at once recognized by the marked upward arching of CuP after leaving the distal angle of the discoidal cell. This character which is, of course, the remnant of the original sigmoidal curvature of this vein, so evident in the Meganisoptera and Protanisoptera, is a very primitive one, derived without change from the Protozygopterous Kennedyidae, in which the same upward arching is clearly to be seen though there is as

yet no true discoidal cell. (Compare figures 4 and 5 with figures 16 and 17.).

The venational characters are as follows:—Discoidal cell with the distal angle more or less acute (in *Perilestes*, its apex is buried in the posterior margin of the wing). Nodus at from one-quarter to one-third of the wing-length from the base; origins of R4 + 5 and 1R3 variable. (*Perilestes* is exceptional in retaining the archaic condition seen in the Permagriidae, in which all the branches of Rs arise well distal to the subnodus.) Pterostigma rectangular or rhomboidal, often with posterior side somewhat swollen into the space below R1; brace vein weak or absent. Supplementary sectors absent or present; formation of transverse arrangements of cross-veins in that part of the wing beyond level of nodus only poorly or partially accomplished; an oblique vein present or absent between R3 and 1R3. Superior anal appendages of male always forcipate.

The final court of appeal to determine whether any particular genus does or does not belong to this family must, I think, lie in the remarkable larval form, in which the labial mask has a prominent cleft median lobe, lateral lobe with two internal teeth only, and no setae either on lateral lobe or movable hooks. Next to the mask of *Hemiphlebia*, this is the most primitive type of Zygopterous mask known. I have recently discovered the larva of *Chorismagrion* in North Queensland and find that it conforms closely to this type also.

This family may be divided into four subfamilies, as follows:—

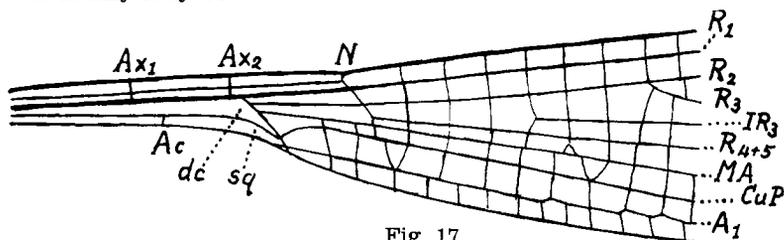


Fig. 17.

Subfamily 1. CHORISMAGRIINAE nov. subfam. Forewing with discoidal cell open basally; all branches of Rs arising well distal to level of subnodus except R4 + 5, which arises at that level.

Only one genus, *Chorismagrion* Morton (Australian).

Subfamily 2. PERILESTINAE nov. subfam. Both wings with discoidal cell closed basally but its distal angle impinging on the posterior border of wing; all branches of Rs arising distal to the level of subnodus.

Only one genus, *Perilestes* Selys. (Neotropical).

Subfamily 3. SYNLESTINAE Tillyard. Both wings with discoidal cell closed basally but the distal angle of cell not extending to wing margin; 1R3 and R4 + 5 arising nearer to subnodus than to arculus.

Two genera, *Synlestes* Selys. (Australian), *Chlorolestes* Selys. (Ethiopian).

Subfamily 4. MEGALESTINAE nov. subfam. Wings as in the Synlestinae except that 1R3 and R4 + 5 both arise nearer to the arculus than to the subnodus.

Two genera, both Oriental, *Megalestes* Selys., *Orolestes* McLachlan.

Annectent forms:—The Megalestinae may be considered, from the venational standpoint only, as annectent to the Lestidae, the corresponding annectent within the Lestidae being the genus *Archilestes*, in which there still remains some indication of the arching of CuP from the distal angle of the discoidal cell. But the very marked differences between the larval characters in the two families Synlestidae and Lestidae seem to indicate that the annectency is not complete—a condition which might easily also be true in supposed fossil annectents, of which we do not know the larval forms.

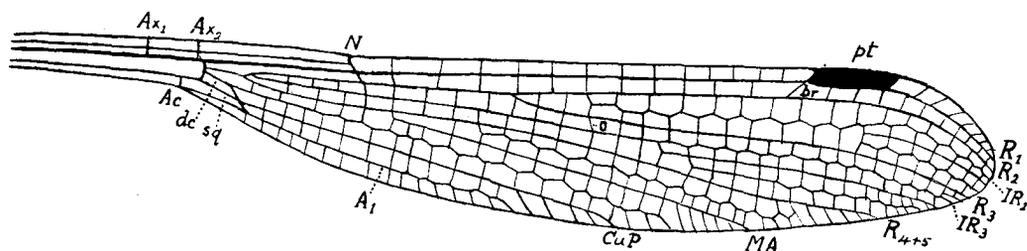


Fig. 18.

Family 3. LESTIDAE auct. (Fig. 18.).

The principal venational characters in this family are the positions of origins of 1R3 and R4 + 5, which both arise much nearer to the arculus than to the nodus, combined with the absence of the principal character found in the Synlestidae, viz., the arching upwards of CuP on leaving the discoidal cell. Most definitions stress the form of the quadrilateral, owing to the fact that, in most of the genera, it is of a characteristic form, with its distal angle very acute and its anterior side much shorter than its posterior one. But this is not true of all the genera, and actually serves, in the present classification, to subdivide the family into two well marked subfamilies.

An oblique vein is invariably present between R3 and 1R3 due to a fixation of a secondary character in the larval wing tracheation.

Of equal importance is the remarkable form of the labial mask of the larva, in which the teeth on the inner margin of the lateral lobe are very large and setae are present both on the lobe itself and the movable hook. The caudal gills are also very characteristic, being very long and with the lateral tracheae placed at right angles to the main tracheal trunks.

In general, the wings of Lestidae are characterized by a considerable lack of alignment of cross-veins transversely across the wing, compared with most other Zygopterid types. This is due to the zigzagging of 1R2 and of the distal portion or even the whole of MA, together with the zigzagging of some of the intercalated sectors, which are present around the distal margin of the wing and more especially between 1R3, R4 + 5 and MA. The pterostigma is always much longer than wide; the subnodal cell is always either completely free from the posterior margin or else merely touches it at its basal posterior angle.

As in the preceding family, the superior appendages in the males are always forcipate.

Two subfamilies can be recognized as follows:—

Subfamily 1. HYPOLESTINAE nov. subfam. Quadrilateral not markedly

acutely angled, its costal side always more than half as long as its posterior side. Pterostigma unbraced.

Only two genera, *Hypolestes* Gund., *Pseudolestes* Kirby, neotropical and Oriental respectively.

Subfamily 2. LESTINAE auct. Quadrilateral acutely angled distally, its anterior side always less than one half the length of posterior side. Pterostigma well braced. Numerous genera are known—*Australestes* Till. (Australian), *Africalestes* Kenn. (Ethiopian), *Archilestes* Selys, *Superlestes* Will., *Cyptolestes* Will. (American), *Platylestes* Selys, *Ceylonolestes* Kenn., *Indolestes* Fraser (Oriental), *Sympecma* Charp. (Eurasian), and *Lestes* Leach (Cosmopolitan).

The Hypolestes are somewhat venationally annectent to the Megapodagriidae. *Archilestes*, as has already been mentioned under the Synlestidae, is venationally annectent to that family. The family Lestidae includes an interesting series of forms with respect to the manner of holding the wings at rest, the more archaic types resting with the wings half-open, the more specialized types with the wings closed.

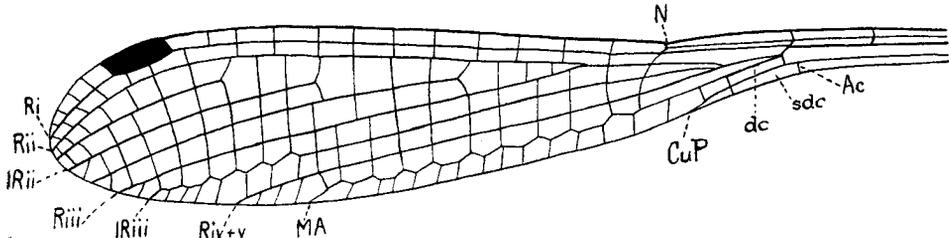


Fig. 19.—*Lestoidea conjuncta* Till.

Family 4. LESTOIDEIDAE NOV. FAM. (Fig. 19.).

Subfam. *Lestoidinae* Munz, 1919, Mem. Amer. Ent. Soc. 3: 17.

This family is proposed for a very remarkable genus, *Lestoidea*, discovered by myself in North Queensland. In it, CuP is reduced to a single cell's length; 1A is entirely absent; 1R3 and R4 + 5 arise together about midway between the arculus and subnodus. Distal to the level of the subnodus, there appear to be four evenly-spaced branches of Rs; of these, the first (most proximal) is obviously R3, the third is almost certainly 1R2, while the second and fourth appear to be two intercalated sectors which have lost their original zigzagging and have become straightened so as to resemble branches of main veins. The only zigzagged veins are the distal

(x) Mr. J. Cowley has pointed out to me that the penile organ of *Pseudolestes* has not the characters of a Lestine one, and that, for this reason, it would be advisable to retain the genus in the Megapodagriidae, an opinion to which I fully subscribe. Again in the case of *Hypolestes*, Kennedy has pointed out that the penile organ has no Lestine characters and closely resembles that of the Amphipteryginae, whilst the larvae resemble those of the Megapodagriidae. In the face of such facts, it seems better to remove these two genera to the Megapodagriidae, and to include only the subfamily Lestinae in the family Lestidae. In the original MS, Dr. Tillyard gives *Ortholestes* Calv., instead of *Hypolestes* Gundlach. Had he had the knowledge of this synonymy, I doubt if he would have suggested such a division of the Lestidae.—Fraser.

third of 1R3 and the greater portion of MA. The pterostigma is considerably longer than wide; discoidal cell an elongate rectangle. The superior anal appendages of the male are forcipate.

Only a single genus, *Lestoidea* Till.

This peculiar form combines the characters found in three different families. The great reduction of the main veins CuP and 1A is reminiscent of the Protoneuridae, the positions of the origins of 1R3 and R4 + 5 resemble those in the Lestidae, and the presence of straight intercalated sectors between R2, 1R2 and R3 reminds one of the Megapodagriidae. *Lestoidea*, however, differs from all known Megapodagriidae, and indeed, from all other Zygoptera, in that these intercalated sectors are carried right through from the wing border to the main stem of R2, so that they exactly resemble in their structure, the vein 1R2 itself.

Family 5. PSEUDOSTIGMATIDAE NOV. fam. (Fig. 20.)

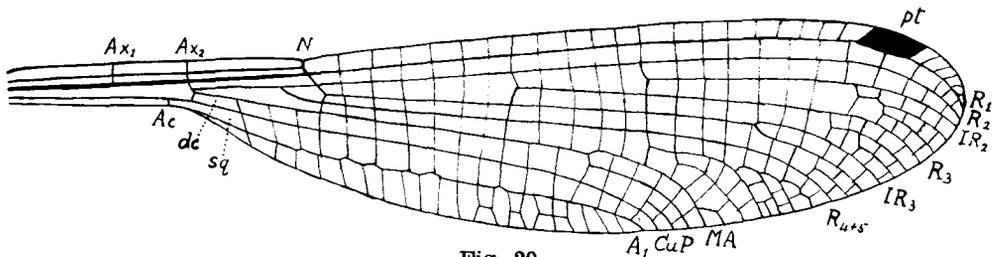


Fig. 20.

Division *Pseudostigmatina* Kirby, 1890, p. 119.

Subfamily *Pseudostigmatinae* Munz, 1919, Mem. Amer. Ent. Soc. 3: 20.

This peculiar and, in some respects, aberrant group can be easily recognized by three important venational characters, viz. (1) the nodus is placed very close to the wing base, i.e., from one-fifth to one-sixth of the total length of the wing (c.f., however *Thaumatoneura*, an annectent genus between this family and the Megapodagriidae), (2) there is an enormous increase in the number of postnodals and generally in the cross-vein system of the whole wing distally from the nodus, and (3) the pterostigma is either absent or extremely aberrant in form, ranging from a group of darkened but not particularly chitinized cells (*Mecistogaster*, *Megaloprepus*) down to a single minute cell in *Microstigma*, and a complete loss of the structure in *Anomisma*.

Other venational characters are:—1R3 arising at the subnodus, R4 + 5 a little before it; 1R2 arising from two to six cells distal to R3; no intercalated sectors present except between R2 and 1R2; discoidal cell simple or crossed, elongate, with the distal angle more or less acute but not markedly so (anterior side always considerably more than half as long as the posterior); veins CuP and 1A always very long, ending up well beyond halfway to apex of wing along the posterior border.

The male appendages are variable in form. The larvae live in water collected at the bases of leaves and bracts of epiphytic Bromeliads in Central and South America; in correlation with this habitat, to allow of their insertion into these deep and cleft-like receptacles, the abdomens of the imagos are greatly elongated.

Genera:—*Mectistogaster* Ramb., *Pseudostigma* Selys, *Microstigma* Ramb., *Anomisma* McLach., *Megaloprepus* Ramb. (xi).

Annectent form:—The family Pseudostigmatidae would appear as a very isolated group in any scheme of classification were it not for the existence of the genus *Thaumatoneura* McLach., here placed in the family Megapodagriidae, but undoubtedly an annectent form connecting the latter with the Pseudostigmatidae. Calvert (1915) has shown that the larva of this genus is a waterfall dweller, and it seems possible that the change from a normal aquatic existence to one in water collected at the base of the leaves of epiphytic Bromeliads, may originally have been accomplished by way of waterfall dwelling? *Thaumatoneura* agrees with the Pseudostigmatidae in the proximity of the nodus to the wing-base and the correlated immense development of postnodals and of the cross-veins in general, distal to the level of the arculus; it agrees with the Megapodagriidae in possessing a well formed, normal pterostigma and in the strong development of intercalated sectors.

While agreeing with Calvert in placing this form definitely within the family Megapodagriidae, I consider it so aberrant in a number of characters that I have no hesitation in forming a separate subfamily for it.

Family 6. MEGAPODAGRIIDAE Till. (Figs. 21, 22.)

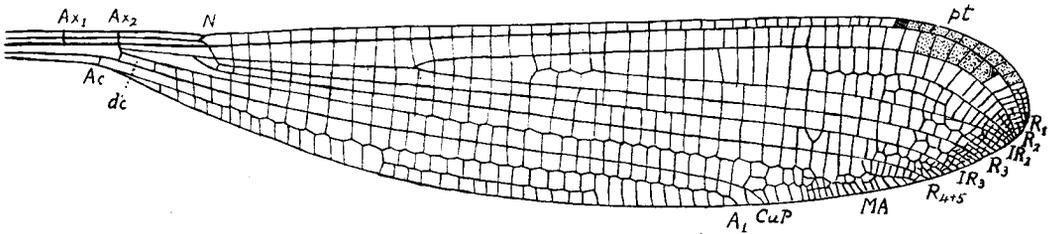


Fig. 21.

This family can be recognized at once by the following combination of characters:—Superior appendages of male forcipate; wings held either open widely or partly so when at rest; venation with a greater or less development of intercalated sectors; $R_4 + 5$ never arising nearer the arculus than to subnodus (equidistant in *Rhipidolestes*, much nearer the subnodus in all other genera); discoidal cell always an elongated quadrilateral, its distal angle varying from acute (*Rhinagrion*, *Megapodagrion*) to subacute in most genera, rectangular in *Thaumatoneura*; $1R_2$ arising from two to four cells distal to R_3 ; pterostigma always complete, variable in shape but usually longer than wide; anal bridge variable, the subdiscoidal cell being either quite separate from the posterior margin of wing or just touching it at the anal crossing, or having its posterior side (the anal bridge) partly or almost wholly fused with that margin; additional antenodals in costal space occasionally present.

Pending the discovery of many unknown larvae in this family, it would

(xi) Kennedy has further split up the genera of this family by characters of the penes, and has created the following extra genera:—*Xanthostigma* Kenn., *Goniostigma* Kenn., *Platystigma* Kenn., and *Haplostigma* Kenn.

appear wisest to abandon any attempt to divide it into subfamilies and, for the present, I shall be content with merely separating *Thaumatoneura* as a distinct subfamily by itself, leaving all the remaining genera in the subfamily Megapodagriinae.

Subfamily THAUMATONEURINAE NOV. subfam. (Fig. 22).

Nodus placed very close to wing-base, at about one-sixth of the length of the wing. Antenodals four to five in number, of which all but the original two are in the costal space only; postnodals extremely numerous; discoidal cell a rectangle; petiole very short. Very great development of arched intercalated sectors along posterior margin of wing; space between 1A and posterior margin very wide distally and with numerous arching branches descending from 1A.

Only one genus, *Thaumatoneura* McLach.

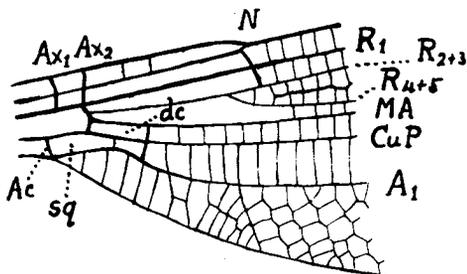


Fig. 22.

Subfamily MEGAPODAGRIINAE McLachlan. (Fig. 21).

Nodus placed at from one-fourth to one-third the length of wing from base; usually only two antenodals but an additional one may be present in some living genera and as many as three additional in the costal space, in some Tertiary genera. Postnodals moderately numerous only; discoidal cell always with the distal angle more or less acute, never an actual rectangle; no marked development of arched intercalated sectors along the posterior margin of wing; space between 1A and the wing border either narrow distally (one cell wide) or at most only moderately wide.

Genera with more than two antenodals:—*Dysagrion* Scudd. (Eocene), *Phenacolestes* Cock. (Miocene), *Neurolestes* Selys. (Recent), *Neuragrion* Karsch. (Recent), *Trineuragrion* Ris. (Recent), *Stenolestes* Scudd. (Miocene).

Genera with only two antenodals (all recent except *Melanagrion* and *Lithagrion*):—*Melanagrion* Cock. (Miocene), *Lithagrion* Scudd. (Miocene), *Rhinagrion* Calv., *Rhipidolestes* Ris, *Podopteryx* Selys, *Argiolestes* Selys, *Podolestes* Selys, *Megapodagrion* Selys, *Mesopodagrion* Selys, *Nesolestes* Selys, *Allopodagrion* Först., *Philogenia* Selys, *Paraphlebia* Hagen, *Allolestes* Selys, *Dimeragrion* Calv., *Heteropodagrion* Selys, *Protolestes* Först., *Heteragrion* Selys, *Mesagrion* Selys, *Burmargiolestes* Kenn., *Caledargiolestes* Kenn., *Celebargiolestes* Kenn., *Agriomorpha* May, *Lestomima* May.

Annectent forms:—I have already indicated *Thaumatoneura* as an annectent form to the Pseudostigmatidae. The genus *Rhipidolestes* is to some extent annectent to the Hypolestinae and Megalestinae (position of origins of 1R3 and R4 + 5), while *Rhinagrion* may perhaps be connected with the original stem of the Lestidae.

The genus *Taolestes* was originally placed by Needham in the family Lestidae, though both the form of its discoidal cell and the remarkable larval characters indicate that it does not belong there (xii). In removing it to the family Megapodagriidae, I also wish to indicate my opinion that this genus represents an archaic type which is to some extent annectant to the more ancient types within the superfamily Agrioidea, more particularly the Amphipterygidae. This problem will be further considered in Part II of this paper.

The Megapodagriinae are, with few exceptions, rare forms concerning which we know very little. Very few of the larval types are known. Until much more has been learnt about them, it will be impossible to disentangle the various lines of evolution within the subfamily.

Family 7. PLATYSTICTIDAE nov. fam. (Figs. 14, 23.).

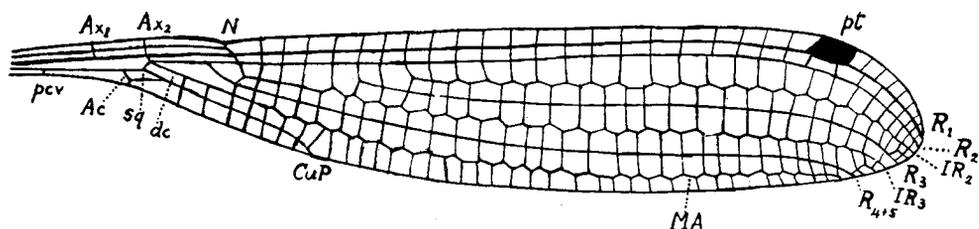


Fig. 23.

Subfamily *Platystictinae* Laidlaw, 1924, *Spolia Zeylanica*, 12: 360.

In the postcubital space (i.e., in the petiole between CuP and the posterior border of the wing) there is a cross-vein situated closer to the base of the wing than to the level of the proximal antennodal; a second postcubital cross-vein, the true *anal-crossing* (Ac) is also present, lying between the levels of the two antennodals and forming a part of the subdiscoidal cell, when that cell is present. Most of the cross-veins situated distal to the nodus are arranged in transverse series, the only breaks being due to zigzagging of veins 1R2, 1R3 and MA. Vein CuP is always reduced and vein 1A absent. No intercalated sectors present; origins of veins 1R3 and R4 + 5 always close to or at the subnodus; veins 1R2 and R3 both comparatively long, arising at least as far from the level of the pterostigma as from the subnodus, usually nearer to subnodus. Nodus at about one-fourth of the wing-length, or a little less. Pterostigma trapezoidal or rhomboidal, never elongate. Discoidal cell rectangular or subrectangular; subdiscoidal cell present or absent; if present, then reduced to a small cell of which the distal angle abuts on to the posterior side of discoidal cell.

(xii) It is unfortunate that Dr. Tillyard was unaware that *Taolestes* Needham is synonymous with *Rhipidolestes* Ris. The latter author correctly placed it near Podagrion, subfamily Megapodagriinae, so that the necessity to remove it to this subfamily does not arise. Moreover, by accepting the larva described by Needham as the larva of *Taolestes*, Tillyard has been led into a maze of errors. Actually this larva is one of Euphaea; probably that of *E. decorata* Selys.—Fraser.

Superior anal appendages forcipate or subforcipate.

Larva with flat, short, subquadrate labial mask, without any setae, the middle lobe cleft; gills triquetral.

The work of Laidlaw and Fraser has shown quite conclusively that this group is well differentiated from the Protoneuridae, with which they had previously been confused owing to the parallel reductions in the veins CuP and 1A. The most important difference, to my mind, is the presence of a very archaic character, viz., the additional, more basally situated post-cubital cross-vein, lying well before the level of the proximal antenodal. It can scarcely be doubted that this represents the cross-vein which originally supported the downturned distal end of the shortened CuA which is present in the Protozygoptera. A comparison of the position of this vein, and of the structure of the subdiscoidal cell, with the corresponding structures in the Protozygopterous family Kennedyidae, indicates clearly enough that we are dealing here with a primitive, reduced offshoot of the ancient Zygopteroid stock. The discovery of the larva by Fraser, with its Gomphid-like labial mask and triquetral gills serves only to confirm this view.

Two subfamilies may be recognized, as follows:—

Subfamily 1. *PALAEMNEMATINAE* nov. subfam. New World forms with 1R2 and R3 arising about midway between the subnodus and pterostigma; CuP not much reduced, ending beyond half-way along posterior border of wing.

Only one genus, *Palaemnema* Selys. (Neotropical.).

Subfamily 2. *PLATYSTICTINAE* Laidlaw. Old World forms with 1R2 and R3 arising nearer to the subnodus than to the pterostigma; CuP markedly reduced, ending at or before half-way along posterior border of wing.

Genera:—*Platysticta* Selys, *Protosticta* Selys, *Drepanosticta* Laid., *Ceylonosticta* Fraser. (All Oriental; no Australian genera.)

It may be noted that the number of postnodals is generally greater in the Platystictidae than in the next succeeding family, but this character has not been included in the definition owing to the fact that the number found in *Drepanosticta* (about fifteen) is equalled by that found in some Protoneuridae, e.g., *Phylloneura*.

In spite of the general resemblance between this family and the next, I doubt whether any true annectants can be indicated. I am inclined to consider that the two families have converged, through reduction of CuP and 1A, and through loss or reduction of the subdiscoidal cell, from two entirely different stocks. I doubt whether the Platystictidae have any close relatives amongst living Zygoptera. On the other hand, the Protoneuridae undoubtedly belong to the old stem of the Coenagriidae and Platycnemididae, and must be considered as a reduced offshoot from an early ancestor of those two families.

The three remaining families of Zygoptera are the Protoneuridae, Platycnemididae and Coenagriidae, in which the dominant impression given by the venation is the high degree of perfection attained by the transverse arrangement of the cross-veins distal to the nodus. Zigzagging of main veins is confined, at most, to the distal portions of 1R2, MA and 1A, so that there is little interruption to the completion of transverse series right across the wing. A few exceptions to this rule are to be noted, in

particular, the genus *Argia*, where the transverse arrangement is disturbed distally due to a slight broadening of the wing and consequent slight proliferation of cross-veins. The superior anal appendages of the males are always specialized, the original forcipate form not occurring. In the larvae, the mask is short and flat, with setae on the lateral lobes. These forms are dominant amongst the Zygoptera, more particularly the Coenagriidae, which can be described as damselflies *par excellence*.

Family 8. PROTONEURIDAE Tillyard. (Fig. 24.).

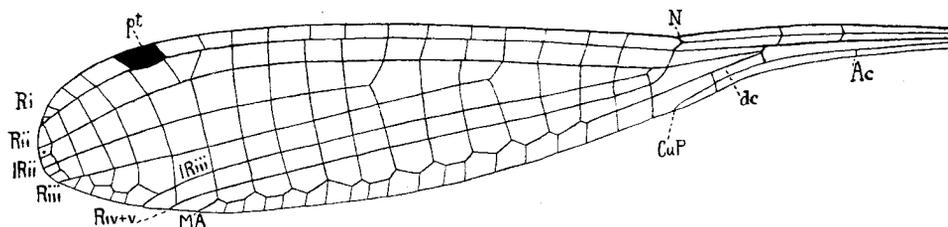


Fig. 24.—*Isosticta banksi* Till.

Protoneuridae Tillyard, 1926, *Insects of Australia and New Zealand*: 76.

No cubital cross-vein present before the level of the proximal antenodal. The sole postcubital nervure present is the anal-crossing (Ac) which lies between the levels of the two antenodals. Discoidal cell a narrow rectangle; subdiscoidal cell complete only in the most primitive genus, *Peristicta*, where its distal side is aligned with the distal side of the discoidal cell. In most forms the subdiscoidal cell is entirely absent and only the anal-crossing is left, but a series of reduction stages can be seen in such genera as *Idioneura*, *Prodasineura*, *Caconeura* and *Esme*, whereby it can be understood that the subdiscoidal cell in this family has undergone changes along entirely different lines from those in the Platystictidae, though both end up at complete suppression of the cell. CuP variable, often reduced; 1A greatly reduced or entirely absent; pterostigma always short, covering from about one-half to one and a half cells in length, variable in shape. 1R3 and R4 + 5 always arise close to subnodus, usually 1R3 at the subnodus and R4 + 5 slightly proximal, but in some genera one or both may arise just distal to the subnodus. 1R3 and R3 always arise well distal to subnodus and are separated by from two to four cells only. Generally all the main veins are straight except only MA, which is more or less zigzagged distally; more rarely 1R3 may be zigzagged for a short distance distally also. Correlated with the foregoing, the transverse arrangement of cross-veins is very complete. The nodus lies usually at about one-third of the wing-length from the base, sometimes a little more or less. Wings generally narrow, the petiole usually slender (rather broad in *Nososticta*).

Superior anal appendages of male very variable, sometimes forcipate (inferiors also sometimes forcipate), more often not. Very few larval types are known, but they appear to agree in the form of the labium, which generally has a cleft median lobe and lateral lobes of the Coenagruid type, with short movable hook, inner margin with teeth small and confined to its distal end, and setae present.

I am unable to subdivide this family into subfamilies. The Old World and New World forms appear to constitute two parallel series with closely similar characters, each still retaining genera with a complete subdiscoidal cell and running out to highly specialized forms with this cell obsolete and CuP greatly reduced.

Genera:—New World Series:—*Peristicta* Selys, *Neoneura* Selys, *Idioneura* Selys, *Microneura* Selys, *Protoneura* Selys, *Epipleoneura* Will., *Epiprotoneura* Will., *Phasnoneura* Will., *Psaironeura* Will.

Old World Series:—*Chlorocnemis* Selys, *Disparoneura* Selys, *Caconeura* Kirby, *Esme* Fraser, *Phylloneura* Fraser, *Melanoneura* Fraser, *Elatoneura* Cowley, *Isomecocnemis* Cowley, *Nososticta* Selys, *Austrosticta* Till., *Neosticta* Till., *Notoneura* Till., *Orosticta* Till., *Selysioneura* Först, *Isosticta* Selys, *Prodasineura* Cowley. Of these, *Nososticta*, *Isosticta*, and all Tillyardian genera are Australian.

Family 9. PLATYCNEMIDIDAE nov. fam. (Fig. 25.).

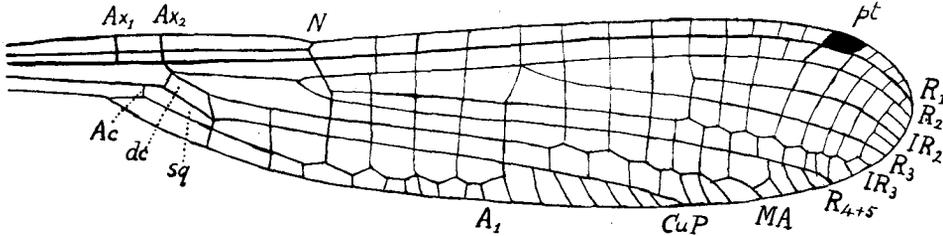


Fig. 25.

Subfamily *Platycneminae* Fraser, 1929, J. Bombay Nat. Hist. Soc., 33: 835.

Nodus situated at about one-third of the wing-length from the base, sometimes slightly more or less but never as close as one-fourth. Pterostigma small, more or less trapezoidal, usually more or less strongly braced. Transverse arrangement of cross-veins distal to subnodus very complete, the only main veins which are zigzagged being 1A, the distal part of MA, and, rarely, the distal part of 1R3. 1R3 and R4 + 5 arising close together at or near subnodus, 1R2 and R3 well distal to nodus and two to four cells apart. Discoidal cell never with the distal angle very acute; either short and rectangular (*Metacnemis*, *Mesocnemis*) or distinctly longer than wide, with the anterior side slightly shorter than the posterior. Subdiscoidal cell always present and complete (absent in *Tatocnemis*). CuP and 1A always well developed.

All species rest with the wings closed. Superior anal appendages of male very variable in form, not forcipate, though the inferiors are sometimes subforcipate. Larvae with labial mask of the Coenagriid shape and type, with median lobe entire, lateral lobes with teeth confined to the distal end, and setae present; caudal gills dilated broadly in their distal portions.

The genera included in this family all belong to the Old World and appear to form a single series beginning with *Metacnemis*, which appears to be annectent in some respects with the Megapodagriliidae, and ending with the extremely petiolate *Tatocnemis*. There appears to be no necessity to subdivide the family into subfamilies for the present. Only a few larval forms are known so far.

Genera:—*Metacnemis* Selys, *Mesocnemis* Karsch, *Calicnemia* Strand, *Stenocnemis*, Karsch, *Platycnemis* Charp., *Copera* Kirby, *Coeliccia* Kirby, *Indocnemis* Laid., *Idiocnemis* Selys, *Paracnemis* Martin, *Leptocnemis*, Kirby, *Allocnemis* Selys, *Tatocnemis* Kirby, *Risio-cnemis* Cowley. This family is unrepresented in Australia.

Family 10. COENAGRIDAE Tillyard. (Figs. 26, 27.).

Family *Coenagriidae* Tillyard, 1926, *Insects of Australia and New Zealand*, 76.

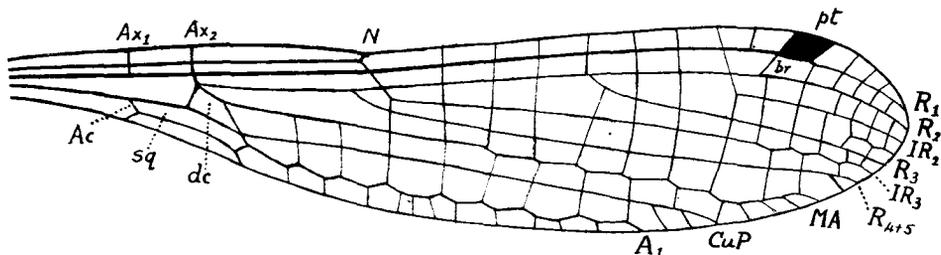


Fig. 26.

This family which is the most successful line of specialization within the whole suborder of Zygoptera, contains a very large number of genera and species, all of which present very much the same general appearance and type of venation. Nodus at about one-third the wing-length from base, never as little as one-fourth. Pterostigma always short, usually covering only one cell, more rarely two, sometimes less than one cell's length, variable in shape but mostly rhomboidal or trapezoidal. Transverse series of cross-veins distal to level of nodus almost always very complete, being only interrupted by the zigzagging of the distal portions of veins MA and 1A, with sometimes additional zigzagging of the distal portion of 1R3 also. Postnodals comparatively few in number, from five to twenty, but usually less than twelve. Veins 1R3 and R4 + 5 arising close together at or near subnodus; in most of the genera, 1R3 arising at the subnodus and R4 + 5 slightly proximal to it. 1R2 and R3 arising more distally, separated by from one to four cells. Discoidal cell with distal angle acute, the anterior side little more than half as long as the posterior. Veins CuP and 1A always well developed. Subcoidal cell always complete, usually entirely free from the posterior margin of wing but sometimes partly sessile on it; in shape it is elongate, from one and a half times to nearly twice as long as the discoidal cell.

Most of the species rest with the wings folded together over the thorax. Superior anal appendages of male never forcipate, usually very short, very variable in form. Larvae with short, flat labial mask, the median lobe entire, the lateral lobes with setae and with the teeth confined to the distal portion; caudal gills either nodate, subnodate or entire, the branch tracheae never at right angles to the main trunks.

While it is impossible to separate out the main evolutionary lines in this huge family satisfactorily, I think that there is still a good deal to be said for Selys original subdivisions, which I propose to recognize as the basis for subfamilies, as follows:—

Subfamily 1. ARGINAE. Petiolation ceasing well before the level of

the anal-crossing (Ac); discoidal cell wider than usual for the family.

Genera:—*Hyponeura* Selys, *Argia* Rambur, *Onychoargia* Selys, *Palaiargia* Först., *Argiallagma* Selys, *Diargia* Calvert (xiii).

Subfamily 2. COENAGRIINAE. Petiolation ceasing a little before the level of the anal-crossing (Ac), so that the subdiscoidal cell still remains complete but the portion of the anal bridge proximal to Ac is much shorter than in the previous subfamily; discoidal cell not widened.

Series A. No spine at the end of the eighth sternite in the female (*Coenagrion* Series):—

Series B. A spine at the end of the eighth sternite in the female (*Ischnura* Series):—

Originally (Biology of Dragonflies, 1917, 280) I divided the subfamily Coenagriinae (portion of my Agrioninae of 1917) into three tribes, the Agrionini, Pseudagrionini and Teinobasini, which together with the Argiini, at that time considered to be only a tribe, made up the complete subfamily. The three tribes mentioned were separated out on the comparative slenderness of the forms, the amount of petiolation of the wings and the position of Ac in relation to the petiole.

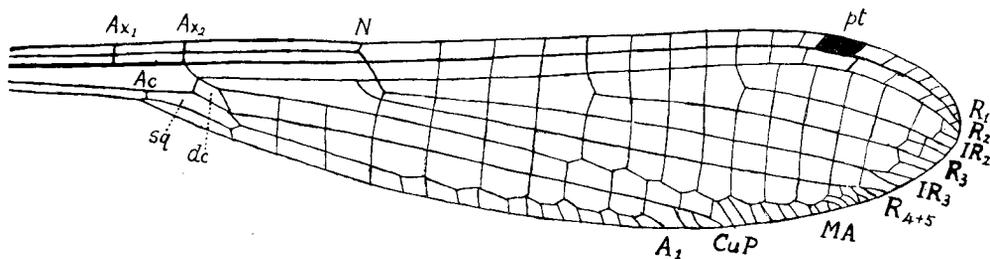


Fig. 27.

At the present time, with our additional knowledge of the evolutionary history of the Zygoptera, it can be seen that the problem of correctly classifying this enormous complex of forms is a purely secondary matter, which can be best undertaken as a separate study by somebody who can gain far more first-hand knowledge of the large mass of non-Australian genera than I can ever hope to do. I do not consider that my classification into tribes represents the true complexities of the evolutionary problem involved in the study of this dominant group. Therefore I shall be content, in this paper, to enumerate (a) the known Australian genera, and (b) the principal non-Australian genera. I might add that, in my opinion, the making of new genera in this group has gone, perhaps, too far, and that modern authors seem to think that genera were intended to indicate only *differences* between species, whereas it should be quite obvious that Linnaeus invented them to emphasize *relationships*.

(xiii) Kennedy has divided up the genus *Argia* into a number of others by employing penile characters: these are—*Chalcargia*, *Cyanargia*, *Heliargia*, *Leptargia* and *Micrargia*.—Fraser.

Australian genera:—*Ischnura* Charp., *Argiocnemis* Selys, *Agriocnemis* Selys, *Caliagrion* Till., *Austroagrion* Till., *Xanthagrion* Selys, *Pseudagrion* Selys, *Ceriagrion* Selys, *Aciagrion* Selys, *Archibasis* Kirby.

Old World genera (in addition to those given for Australia):—*Coenagrion* Kirby, *Pyrrhosoma* Charp., *Erythromma* Charp., *Nehalonia* Selys, *Thermagrion* Förster, *Mombagrion* Sjöst., *Argiagrion* Selys, *Xiphiagrion* Selys, *Teinobasis* Kirby, *Mortonagrion* Fraser, *Enallagma* Charp., *Himalagrion* Fraser.

New World genera:—*Amphiagrion* Selys, *Tigriagrion* Calv., *Hesperagrion* Calv., *Chromagrion* Need., *Anomalagrion* Selys, *Oxyagrion* Selys, *Acanthagrion* Selys, *Anisagrion* Selys, *Telagrion* Selys, *Leptagrion* Selys, *Megalagrion* McLach., *Hylaeagrion* Förster, *Aeolagrion* Will., *Antiagrion* Ris, *Telebasis* Selys, *Metaleptobasis* Calv., *Ceratura* Selys, etc.

In addition, it should be noted that the genus *Ischnura* is practically cosmopolitan and that *Coenagrion* and *Enallagma* are widely spread throughout the Northern Hemisphere.

(To be continued.)

EXPLANATION OF TEXT-FIGURES.

1. *Dictyoptilus sepultus* Handl., Order Palaeodictyoptera. (Considered by Lameere to belong to the Odonatoid Orders, Group Stenodictyoidea.) Crossveins omitted for the sake of clarity. Convex veins shown thick to distinguish them from concave ones shown thin. *C*, costa, *Se*, subcosta, *Ri* radius, *Rs*, radial sector, *M*, anterior median, *MP*, posterior median, *CuA*, anterior cubitus, *CuP*, posterior cubitus, *1A*, first anal vein, *pca*, precostal area, *AxP*, axillary plate.
2. Odonatoid type of wing, base only shown. *AxP*, axillary plate.
3. *Protagrion audouini* Brong., Wing. Order Protodonata, family Protagriidae. (Upper Carboniferous of France.) *Rii*, *Riii*, and *Riv* + *v* principal branches of *Rs*. Other lettering as for Fig. 1.
4. *Typus permianus* Sell. Forewing. Order Odonata, suborder Meganisoptera, family Meganeuridae. Cross veins omitted for sake of clarity. Lettering as for Fig. 1.
5. *Megatypus schucherti* Till. Basal portion of hindwing with cross-veins included. *Ac*, anal crossing, *mb*, membrane. Other lettering as for Fig. 1. Note the basal remnants of *Mp* and *CuA*. Same Order and suborder as *Typus permianus*, family Meganeuridae.
6. *Kennedyia mirabilis* Till., Wing. Order Odonata, suborder Protozgyoptera family Kennedyidae. (Lower Permian of Kansas.) Note the basal remnant of *CuA* with its supporting cross-vein *pcv*. *Sq*, subquadrilateral or subdiscoidal cell, *pt*, pterostigma, *1Rii* and *1Riii*, intercalated nerves. Other lettering as for previous figures.
7. *Permagrion falklandicum* Till., Wing. Order Odonata, suborder Zygoptera, family Permagriidae. (Upper Permian of Falkland Islands.) *dc*, discoidal cell (an open one in this wing), *nv*, nodal vein, *snv*, subnodal vein. Other lettering as for previous figures.

8. *Permolestes gracilis* Martyn., Wing. Order Odonata, suborder Protozoptera, family Permolestidae. (Permian of Russia.) Lettering as for previous figures. Note here also the basal remnant of *CuA* and its supporting vein *pcv*.
9. *Kennedya mirabilis* Till. Details of wing.—A. The petiole showing the faint basal portion of *Rs* + *MA* running below and parallel to *Ri*. Note the basal remnant of *CuA* supported below by the postcubital vein *pcv*. *Avi*, proximal primary antenodal vein. B. Region of the arculus and discoidal cell. *Ac*, anal crossing, *arc*, arculus, *Ax2*, distal primary antenodal nervure, *dv*, discoidal cross-vein, *sq*, subdiscoidal cell. Other lettering as for previous figures.
10. *Protomyrmeleon handlirschi* Martyn. Forewing. Order Odonata, suborder Archizyoptera. (Jurassic of Turkestan.) Lettering as for previous figures.
11. The Costo-antenodal Complex. *C*, costa, *Sc*, subcosta, *R* + *M*, radial sector plus anterior media, *pan*, primary antenodal nervures, *san*, secondary antenodal nervures, *N*, nodus. The three figures demonstrate the gradual evolution from two solitary primitive antenodal nervures to the recent condition where these have been entirely replaced by the steady addition of weaker secondary antenodals.
12. *Hemiphlebia mirabilis* Selys. Forewing. Suborder Zygoptera, family Hemiphlebiidae. Lettering as for previous figures. Note the discoidal cell, *dc*, which is here an open one (but closed in the hindwing). Note also the vein *Ai* (1A) which is continued basalwards to run along the posterior border of wing. Lastly note that the postnodal nervures do not coincide with the cross-veins below them.
13. *Hemiphlebia mirabilis* Selys. 1-4 and 6. Base of wing enlarged to show the variable conditions of the anal-crossing and nervure 1A met with. Note in Fig. 4 the presence of an apparent postcubital nervure similar to that found in the family Platystictidae. 5. Base of wing of *Agrionemis pygmaea* (Ramb.) contrasted with the hindwing of *Hemiphlebia mirabilis* shown in 1 and 2.
14. *Platysticta deccanensis* Laidlaw. Basal portion of forewing, enlarged to show the postcubital vein, *pcv*, anal-crossing *Ac*, and subquadrangle, *sq*. Suborder Zygoptera, superfamily Coenagriioidea, family Platystictidae. (Recent, India.) (Adapted from Fraser.)
15. *Permagrion falklandicum* Till. Wing, probably a forewing. Suborder Zygoptera, superfamily Coenagriioidea, family Permagriidae. Lettering as for previous figures. (Upper Permian, Falkland Islands.)
16. *Synlestes weyersi* Selys. Forewing. Suborder Zygoptera, superfamily Coenagriioidea, family Synlestidae. (Recent Australia.) Lettering as for previous figures, except *o*, oblique vein.
17. *Chorismagrion risi* Morton. Basal portion of forewing. Suborder Zygoptera, superfamily Coenagriioidea, family Synlestidae. (Recent, Australia.) Note the open discoidal cell, *dc*. In the hindwing, this cell is closed in the normal way.
18. *Austrolestes cingulatus* Burm. Forewing. Suborder Zygoptera, superfamily Coenagriioidea, family Lestidae. (Recent, Australia.) Lettering as in previous figures, except *o*, oblique vein.
19. *Lestoidea conjuncta* Till. Forewing. Suborder Zygoptera, superfamily Coenagriioidea, family Lestoideidae. (Recent, Australia.) Lettering as

- in previous figures. Note the reduction of *CuP*, absence of *1A*, and the presence of an additional sector between *R2* and *1R2*.
20. *Pseudostigma aberrans* Selys. Hindwing (adapted from Munz). Suborder Zygoptera, superfamily Coenagriioidea, family Pseudostigmatidae. (Recent, Central America.) Lettering as for previous figures. Note the position of the nodus and the degradation of the pterostigma.
 21. *Argiolestes icteromelas* Selys. Forewing. Suborder Zygoptera, superfamily Coenagriioidea, family Megapodagriidae. (Recent, Australia.) Lettering as for previous figures.
 22. *Thaumatonaura pellucida* Calvert. Basal portion of forewing (adapted from Munz). Suborder Zygoptera, superfamily Coenagriioidea, family Megapodagriidae. Lettering as in previous figures. Note the additional antenodals, not passing down on to *R1* (secondary antenodals). (Recent, Central America.)
 23. *Platysticta deccanensis* Laidlaw. Complete forewing. Lettering as in previous figures. (See Fig. 14.)
 24. *Isosticta banksi* Till. Hindwing. Suborder Zygoptera, superfamily Coenagriioidea, family Protoneuridae. (Recent, Australia.) Note the absence of the nervure *1A* and the reduction of *CuP*. Lettering as for previous figures.
 25. *Platycnemis latipes* Selys. Forewing. Suborder Zygoptera, superfamily Coenagriioidea, family Platycnemididae. (Recent, South Europe and Central Asia..) (Adapted from Fraser.)
 26. *Coenagrion dyeri* Fraser. Hindwing. Suborder Zygoptera, superfamily Coenagriioidea, family Coenagriidae. (Recent, India.) (Adapted from Fraser.) Lettering as for previous figures
 27. *Pseudagrion australasiae* Selys. Forewing. Suborder Zygoptera, superfamily Coenagriioidea, family Coenagriidae. (Recent, Australia.) Lettering as for previous figures
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