

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

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CONTINUATION AND CONCLUSION.

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PART III.

Suborder ANISOZYGOPTERA.

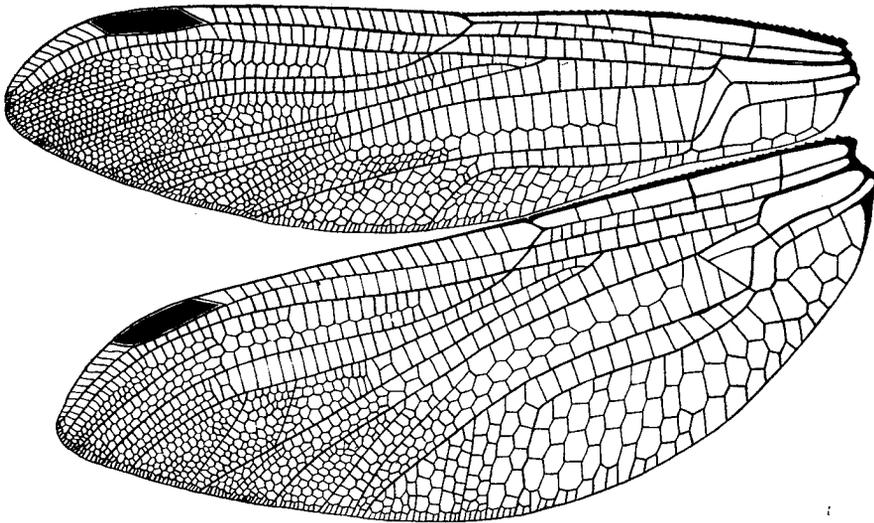


Fig. 1.—Wings of *Heterophlebia buckmani* (Brodie) (*Anisozygoptera*).

The suborder *Anisozygoptera* includes a single recent and a number of Mesozoic genera in which anisopterous and zygopterous characters are found mingled in varying proportions. It marks the transition of the suborder *Anisoptera* from the *Zygoptera*, so that if we examine the extremes of the types, we find at the one end, forms in which zygopterous characters predominate, and at the other, forms which are definitely anisopterous in facies. The whole of the forms found in the Lias belong to the latter category and Tillyard considered that the suborder *Anisozygoptera* should be restricted to include these. Carpenter would further restrict the suborder to include only those forms in which the discoidal cell of the hindwing is divided by a traversing nervure into two cells and differs markedly in shape from that of the forewing. Such a classification would exclude, of

course, the vast majority of the forms and neither author has suggested a new suborder for the inclusion of these.

Nor do I think that a new suborder is required since all the forms which would be excluded possess a mingling of zygoterous and anisopterous characters which is just what Handlirsch implied by his name Anisozygoptera. Of the Jurassic forms, *Tarsophlebia eximia* Hagen, has the base of the hindwing much broader than that of the forewing and there is a marked difference in the shape and inclination of the discoidal cells—both anisopterous characters—for the rest, the long slim abdomen and the long, slender, spider-like legs are zygoterous in nature; *Isophlebia aspasia* Hagen, on the contrary, has the legs short and robust like a Gomphine, and the anal appendages are of distinct Petalurine shape and character—it is a very aberrant form and might equally well belong to the Zygoptera or Anisoptera; *Stenophlebia aequalis* Hagen (Fig. 4c) has the eyes so close together that its head might well belong to a Libelluline; apart from this, its characters are mainly zygoterous. Examples like this may be multiplied, so that I consider a reclassification unnecessary, premature in the present state of our knowledge and possibly artificial if founded on uncertain characters.

If we examine the discoidal cells in any of the Liassic forms of the *Anisozygoptera*, we shall note that the antero-distal angle of the cell in the forewing is obtuse, but in that of the hindwing, either right-angled or more or less acute. This latter has been brought about by a broadening of the hindwing by which the main nervures MA and CuP diverge. In the Jurassic forms, the broadening of the cell is particularly marked, even where the shape and inclination of the two cells differ in the wings, and therefore the antero-distal angle of the cell in the hindwing is always obtuse. In this character then, we have a means for splitting the suborder *Anisozygoptera* into two superfamilies: the *Tarsophlebioidea* in which the antero-distal angle of the discoidal cell of the hindwing is obtuse, and the *Heterophlebioidea*, in which the same angle of the cell of the hindwing is always acute. I include in this latter the genus *Epiophlebia*, although it is an exception to the rule, but in it, the discoidal cell of the hindwing is often traversed by a nervure as in *Heterophlebia*, and, moreover, the shape of this cell conforms closely to that of the rest of the forms in the superfamily.

*Epiophlebia* is represented by two recent species, one, *E. superstes* (Selys) which is confined to Japan, being known from both imago and larva, the other, *E. laidlawi* Tillyard, from the larva only. The former species is perhaps the most interesting living form in the whole of the order *Odonata*, for in it we find two different forms illustrating how the discoidal cell, as it exists in the Anisoptera, came to be divided. In a recent paper (1938, Proc. R. ent. Soc. (A), 13: 155) I have shown that two different systems of venation are found in the species (Fig. 2, 1-3), in one of which the arculus of the fore and hindwings is similar and the discoidal cell of

Fig. 2.—Discoidal cell of:—(1) *Epiophlebia superstes* (Selys), forewing. (2) The same: Forma 1, hindwing. (3) The same: Forma 2, hindwing; note the cell is here divided. (4) *Liassophlebia magnifica* Tillyard, hindwing. (5) *Heterophlebia buckmani* (Brodie), forewing. (6) The same: hindwing. Compare with 4.

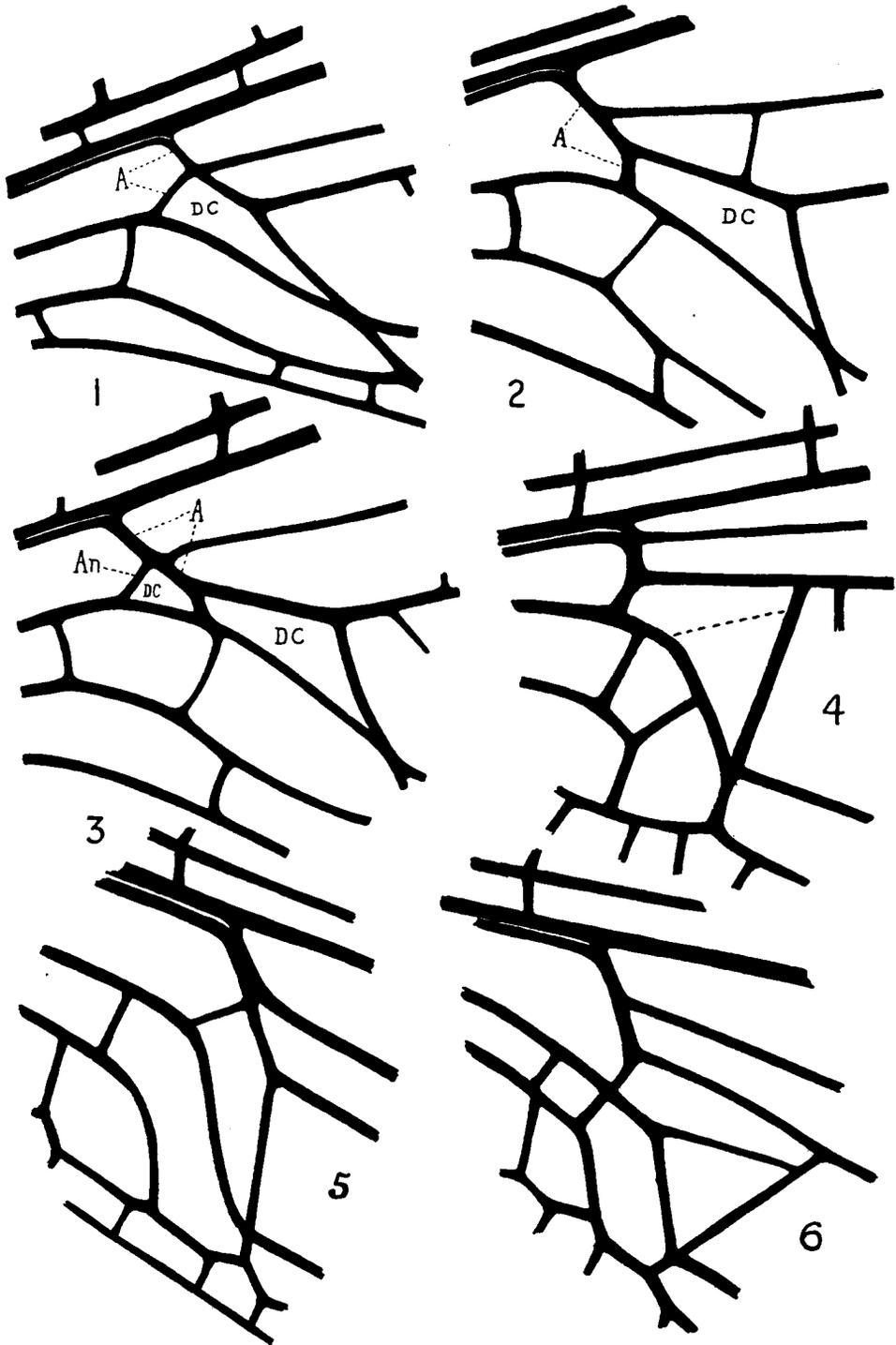


Fig. 2.

the hindwing is crossed and divided by an oblique vein. In the other form, the lower arculus is absent, its place or function being taken by the above-mentioned oblique vein. The first form thus agrees with the Liassic genus *Heterophlebia* in having a simple zygopterous undivided cell in the forewing, and a dilated, divided anisopterous cell in the hindwing. It seems clear that the dividing vein was acquired originally to take the place of the lower arculus, but that both were retained in some forms which ultimately gave rise to the *Anisoptera*. From the shape of the discoidal cell in the hindwing of *Liassophlebia magnifica* Tillyard (Fig. 2, 4), I feel convinced that if we had a series of specimens available, we should find that two forms of venation existed similar to those found in *Epiophlebia*; similarly, in forms like *Petrophlebia anglicana* Tillyard, the existing lower arculus may represent a more distal vein which has taken the place of the original lower arculus.

In *Progonophlebia woodwardi* Tillyard, the structure of the base of the discoidal cell and the arculus is obscured but the poorly preserved vein at the base of the former does not appear to represent the lower arculus and there is the beginning of another vein more proximal to it. In *Progonophlebia brodiana* sp. nov. (= *Anisopteron brodianum* Handl.) the base of the discoidal cell is more proximal and there is another cross-vein in the median space proximal to it, which may indicate a division of the cell as in *Epiophlebia*. (It is unfortunate that Dr. Tillyard overlooked this species and that Handlirsch failed to recognise the genus to which it belonged.)

I do not propose to discuss here the forms belonging to the *Tarsophlebioidea* since they represent blind alleys and all species became extinct. Of the *Heterophlebioidea*, apart from *Epiophlebia*, the various species of the genus *Heterophlebia* Westwood, are the most important since the venation of the wings gives us a graphic description of the transition of the *Anisoptera* from the *Zygoptera*. (Fig. 1.) In the forewing, the base of which is very narrow, the discoidal cell is a narrow, acutely angled quadrangle such as we find in any of the small damsel-flies of to-day; its formation could not be more typically zygopterous. We note only that the arculus has recessed and now occupies a position nearly midway between the primary antenodals, and that the two sectors Riv + v and IRiii have recessed to a degree somewhat less than what we find in the *Amphipterygidae*. The antenodal complex is however a very close copy of what we find in this latter family, viz., in such forms as *Diphlebia*, etc. (In *Epiophlebia* the antenodal complex has advanced a stage beyond *Heterophlebia* and resembles that found in the anisopterous family *Gomphidae*.) In the hindwing of *Heterophlebia* the discoidal cell is very different from that of the forewing, and in shape and by its division into two cells, is as much an anisopterous structure as the cell of the forewing is a zygopterous one. Moreover, the base of the hindwing is greatly broadened as in the *Anisoptera*. The whole story of the descent of the *Anisoptera* from the *Zygoptera* is written in the venation of the wings and the anatomy of this genus and other Liassic dragonflies, for it was necessary that there should be a mingling of zygopterous and anisopterous characters in the passage from one to the other. The presence of such transitional forms is quite meaningless if we accept Carpenter's theory of the origin of the *Anisoptera* from some Permian Protanisopterous ancestor.

The classification of the suborder *Anisozygoptera* is as follows:—

## Suborder ANISOZYGOPTERA Handlirsch.

## Family TARSOPHLEBIOIDEA.

- Family 1. *Tarsophlebiidae* Handl. Genera: *Tarsophlebia* Hagen, *Tarsophlebiopsis* Till., *Karatawia* Martyn.
2. *Isophlebiidae* Handl. Genera: *Isophlebia* Hagen, *Anisophlebia* Handl.
3. *Mesophlebiidae* Handl. Genera: *Mesophlebia* Tillyard, *Triassophlebia* Tillyard.
4. *Sublosiidae* Handl. Genera: *Sublosia* Handl. (Oligocene).  
Inc. sed.: *Heterothemis* Handl., *Liadothemis* Handl., *Oryctothemis* Handl., *Palaeophlebia* B., R. & G., *Parelothemis* Handl., *Perissophlebia* Tillyard, *Petrothemis* Handl., *Anormothemis* Handl., *Systellothemis* Handl., *Rhabdothemis* Handl., *Pycnothemis* Handl., *Temnothemis* Handl.

## Superfamily HETEROPHLEBIOIDEA.

- Family 1. *Liassophlebiidae* Tillyard. Genera: *Liassophlebia* Tillyard.
2. *Archithemidae* Handl. Genera: *Archithemis* Handl., *Petrophlebia* Tillyard, *Diastatommities* Handl., *Campterothlebia* Bode, *Selenothemis* Handl.
3. *Progonophlebiidae* Tillyard. Genera: *Progonophlebia* Tillyard.
4. *Heterophlebiidae* Handl. Genera: *Heterophlebia* Westwood.
5. *Epiophlebiidae* Tillyard. Genera: *Epiophlebia* Calv.
6. *Liassogomphidae* nom. nov. Genera: *Liassogomphus* Cowley.

Dr. Tillyard, in his "British Liassic Dragonflies", p. 12, has treated *Petrophlebia* as a separate family, giving as his reasons the absence of the two "hypertrophies antenodals", but although the primary antenodals cannot be made out in the fossil, it is certain that they must be present since these two structures are ordinal characters and are only found suppressed in the most recent families of the *Zygoptera* and *Anisoptera*. For this reason I have merged it with the *Archithemidae*. In a revision of the work quoted, I feel sure that the author would have merged the two families, for he says:—"In spite of the given venational differences, it seems to me that this genus is very closely related to *Diastatommities* Handl. (*Archithemidae*) which it greatly resembles in the form of the discoidal field and the cubito-anal area".

## Suborder ANISOPTERA.

The suborder Anisoptera is divided up into six families containing forms which, in regard to their wing venation and powers of flight, show the highest development yet attained in the order *Odonata*. All six families agree in having the discoidal cell of both wings divided into two, an anterior or "hypertriangle" and a posterior or "discoidal triangle". The latter may be again split up into two or more cells by traversing veins and, indeed, in some species is made up of a dense reticulation of veinlets. Even in the latter, however, the original dividing vein or veins may be made out as a rule. The base of the hindwing is usually considerably broadened, but in the supposedly archaic forms this may be either not marked or altogether absent, though the wings are never petiolated as in the *Zygoptera*. The pterostigma is invariably present in both fore and hindwings and is usually

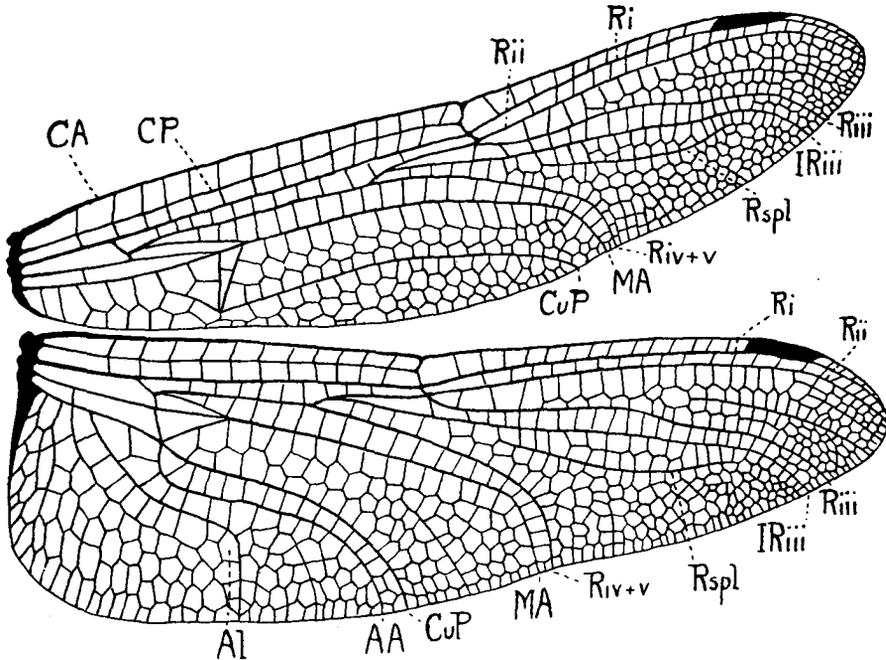


Fig. 3.—Wing of an Anisopterous dragonfly (*Libellulidae*). AA.—Analis anticus. Al.—Anal-loop. CA.—Costalis anticus. CP.—Costalis posticus (Sub-costa). CuP.—Cubitus posticus. Rspl.—Radial supplement. R.—Radius and its branches. MA.—Medianus anticus.

of elongated, Lestine shape and braced or unbraced. Except in the *Libellulidae* and a few aberrant recent genera of the *Aeshnidae* and *Corduliidae*, the base of the hindwing in the male is more or less angulated and excised, but it is always rounded in the female of all families.

The eyes exhibit a wide differentiation from being widely separated in the *Gomphidae*, more slightly so in the *Cordulegasteridae* and *Petaluridae*, to a wide confluence across the middle line of the head in the other families. They reach their greatest size and confluence in the *Aeshnidae*. Since separation of the eyes is common to the whole of the suborder *Zygoptera*, its presence in these three families must be regarded as an archaic character, and the *Gomphidae*, in which it is most pronounced, the most archaic of all the six families.

The shape of the abdomen exhibits an even greater differentiation, even within individual families; thus in the *Libellulidae* the abdomen may be longly or shortly cylindrical, longer or shorter than the wings, fusiform or tapered to the end, strongly carinated on the dorsum or markedly depressed. In many females, the 8th and 9th segments are foliately dilated, and this specialisation appears to be the outcome of the loss of the primitive zygopterous ovipositor, the lateral expansions of the segments taking on its function.

In general, the secondary sexual apparatus of the male is similar to that of the *Zygoptera*, although perhaps more highly specialized. The

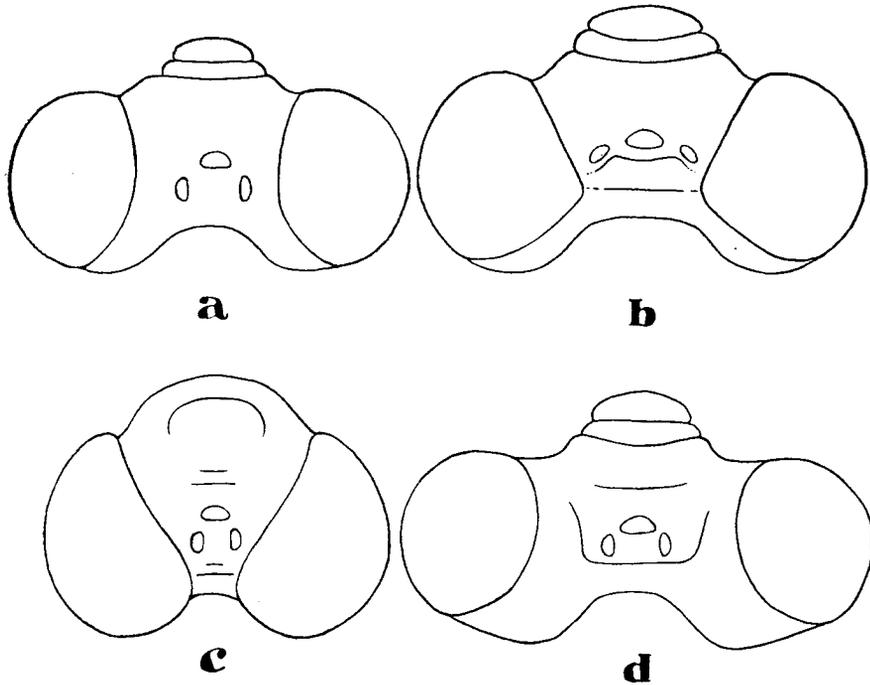


Fig. 4.—Outline of heads of:—(a) *Heterophlebia buckmani* (Brodie). (b) *Heliogomphus promelas* (Selys). (c) *Stenophlebia* sp. (The head is somewhat distorted from pressure.) (d) *Epallage fatima* Charp.

female genitalia, however, exhibits various stages of evolution, the *Aeshnidae* and *Petaluridae* still retaining the zygopterous ovipositor, whilst this organ is present in a degraded condition in the *Cordulegasteridae* and entirely absent or atrophied in all the other families. It may be said that if the female genitalia be taken as a criterion, then the *Aeshnidae* are every bit as archaic as the *Gomphidae*.

In the face of such equivocal evidence, it is necessary to seek elsewhere for characters by which the relationships and phylogeny of the six families may be interpreted. Fortunately we find such characters exhibited by the larval forms belonging to the various families, many of which are now well known.

The general shape of the larvae differs markedly between the families and, in the case of the *Gomphidae*, within the family itself. It is only when we come to look into details that we find a greater homogeneity exists, especially in such organs as the labium and the gizzard. By employing these latter, it is possible to establish relationships between the families and even between these and the *Zygoptera*.

#### The Labium. (Fig. 5.)

Two very definite types of labium exist in the Anisopterous larvae—a flat type which closely resembles that of the *Zygoptera* and which has obviously been derived from that suborder, and a cupped or deeply concave

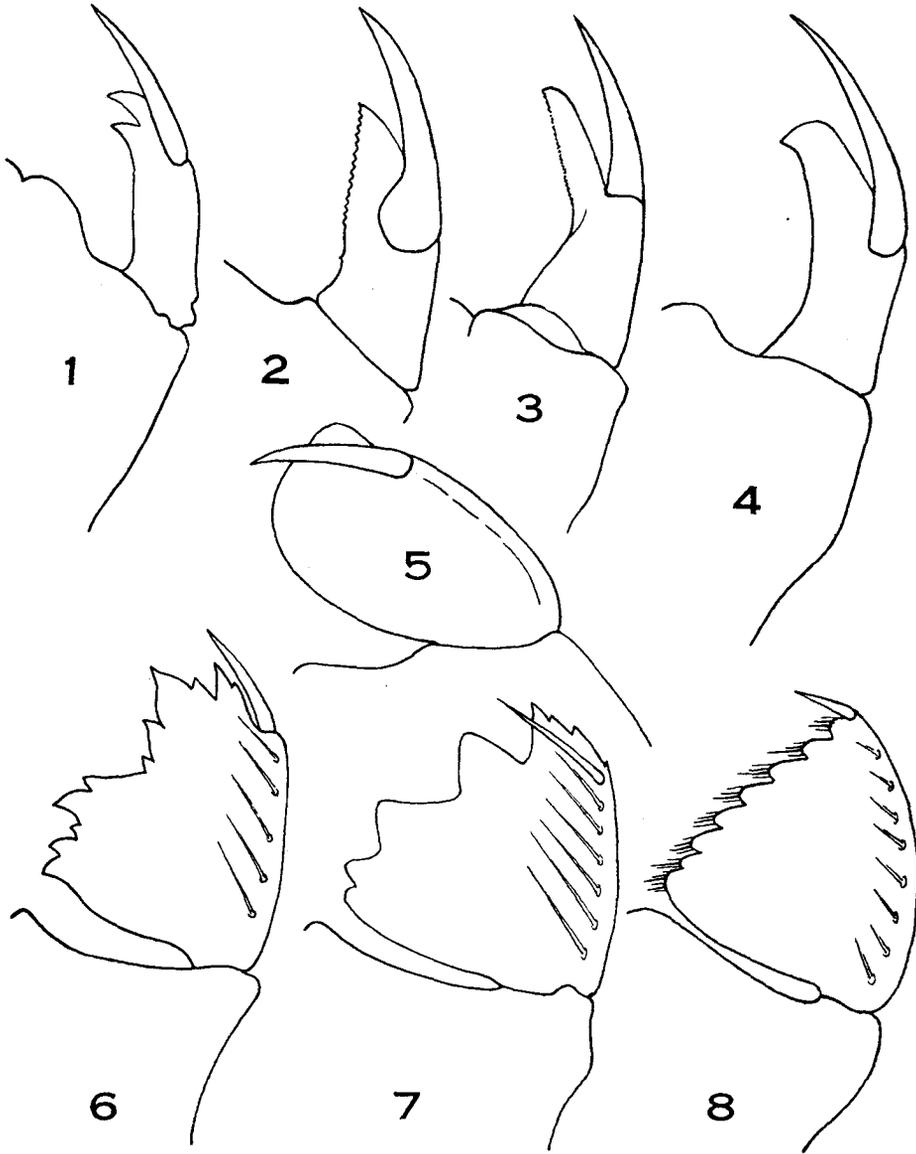


Fig. 5.—Labial masks of:—(1) Agrionine. (2) Austrogomphus. (3) Austropetalia. (4) Aeshna. (5) Petalura. (6) Cordulegaster. (7) Synthemis. (8) Libelluline.

type, which is a recent development peculiar to the *Anisoptera*. To the former type belong the *Heterophlebiidae* of the *Anisozygoptera* as evidenced by the larva of *Epiophlebia*, the only living forms belonging to this sub-order; in it the labium is almost identical to that of the *Gomphidae*, differing only by the shorter and less robust movable hook, which, of course, is a zygoterous character. To this type also belong the *Gomphidae* and *Aeshnidae* which are thus seen to be the most archaic of the Anisopterous families. The *Petaluridae* possess a labium which conforms to neither type, but which, from its shape, appears to show a passage from the flat to the concave type; an appearance which, I think, is more apparent than real. From the small size of the movable hook as compared to that of the lateral lobe, the inclination appears to be towards the *Anisoptera*. The remaining three families *Cordulegasteridae*, *Corduliidae* and *Libellulidae* all belong to the concave type. The *Cordulegasteridae* labium has the lateral lobe broadly triangular and deeply serrate and biserrate along the inner border; the primitive *Corduline* larva is very similar to this but lacks the biserrations. A study of the labia in the Australian genera *Cordulephya*, *Synthemis*, *Choristhemis* and *Eusynthemis* reveals a complete series which exhibits serrations as deep as those in *Cordugaster*, to others in which they begin to assume the crenately bordered labia of the higher *Corduliidae* and *Libellulidae*. Another similarity between *Synthemis* and *Cordulegaster* must be mentioned here, viz., the presence of a frontal plate on the head, a character shared only by these dragonfly larvae.

The Gizzard. (Fig. 6.)

The gizzard of Odonate larvae has the lining membrane gathered up into a number of folds varying from 16 in the primitive *Zygoptera* and *Anisozygoptera* (*Epiophlebia*) to 8 or 4 in the *Anisoptera*. The folds are armed with chitinous teeth numbering from 20 to 1, and are alternately long and short where the folds are numerous. The reduction in the number of folds has probably been brought about by suppression of the minor folds or by an amalgamation of these folds with the major ones, thus the exact stage at which this evolutionary process has arrived at in the various families is of great phylogenetic significance. The reduction in the number and the shape of the teeth is of equal importance. In the imago, the gizzard exists as an atrophied structure and the dentition is either greatly reduced as in the *Zygoptera* or altogether lost as in the *Lestidae* and *Anisoptera*. In this we see yet another link established between a Lestid form of ancestor and the *Anisoptera*. The *Zygoptera* and *Anisozygoptera* stand at the foot of the series with 16 folds armed with numerous teeth; the *Petaluridae* follow with 8 folds but armed with only one or two teeth; the remaining families of the *Anisoptera* have only 4 folds, but these, in the *Gomphidae*, are furnished with numerous teeth as in the *Zygoptera*. The *Aeshnidae* show a great reduction in the number of teeth which are more specialized and much more robust in character. Finally the *Cordulegasteridae*, *Corduliidae* and *Libellulidae* have but one tooth per fold, thus paralleling the evidence afforded by a study of the larval labium.

One other important character remains to be discussed, viz., the presence of membranous keel-like armature on the tibiae of the *Chlorogomphinae* (*Cordulegasteridae*) and the *Corduliidae*. Taken in conjunction with the evidence afforded by the labial mask, the frontal ridge and the form of the gizzard, these tibial keels seem to me to indicate a descent of the higher *Anisoptera* (*Corduliidae* and *Libellulidae*) from a *Cordulegasterine* ancestor, and a common origin with the *Chlorogomphinae*.

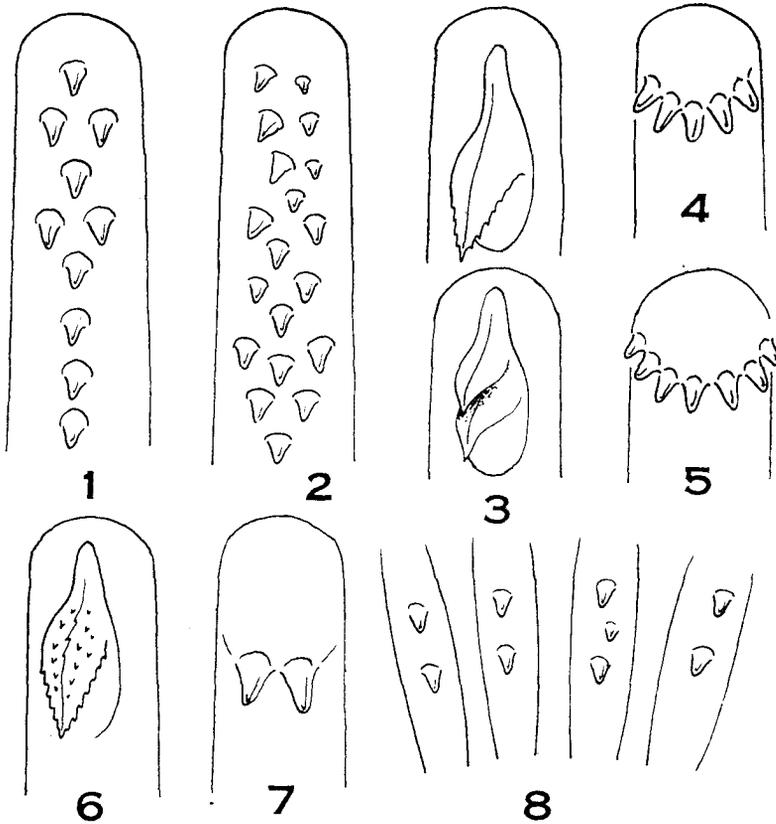


Fig. 6.—Gizzard armature in:—(1) Amphipterygine (*Diphlebia*). (2) Gomphine (*Austrogomphus*). (3) Corduline and Libelluline. (4) Lestine (*Austrolestes*). (5) Aeshnine (*Aeshna*). (6) Cordulegasterine (*Chlorogomphus*). (7) Petalurine (*Petalura*). Four of the 8 folds are shown of this last.

To sum up the evidence, it would appear that the *Gomphidae* have adhered most closely to the ancient Anisozygopterous line, the only living descendants of which are the two species of *Epiophlebiasuperstes* (Selys) and *laidlawi* Tillyard. The *Aeshnidae* and *Petaluridae* arose later from the *Anisozygoptera* and still inherit some zygoterous characters which had been preserved in that ancient line after the departure of the *Gomphidae*. From this Aeshnid line arose the *Cordulegasteridae* which later threw off the common ancestor of the *Chlorogomphinae* and *Corduliidae*, from the latter of which arose the *Libellulidae*.

#### The Fossil history of the *Anisoptera*.

The *Anisoptera* first make their appearance in the Jurassic, where are found forms which are closely related to the present-day *Gomphidae*, *Petaluridae* and *Cordulegasteridae*. The problematical form *Liassogomphus brodei* (Buck), which Handlirsch and Tillyard placed in the *Gomphidae* but

which the latter subsequently relegated to the *Anisozygoptera*, I would regard as an annectant form between that suborder and the *Gomphidae*; apart from this, no *Anisoptera* are known from the Liassic. In the Cretaceous, only a single dragonfly is known, which is probably related to the *Aeshnidae*. From the Tertiary deposits a large number of Anisopterous forms are known, most of which so closely resemble those of to-day, that they are of small use for tracing the phylogeny of the latter. The *Libellulidae*, the most recent of all Odonata, are first found in the Miocene, if we except a single Corduline genus from the Oligocene of N. America.

Key to the families of the *Anisoptera*.

- |    |   |   |                            |
|----|---|---|----------------------------|
| 1. | { | Antenodal complex complete; primary antenodals absent or atrophic. . . . .  | 5.                         |
|    | { | Antenodal complex incomplete; primary antenodals well-defined. . . . .  | 2.                         |
| 2. | { | Eyes broadly contiguous over middorsum of head; discoidal cells of fore and hindwings of similar shape and situated equally far from the arculus; female with a complete zygopterous ovipositor . . . . .   | <i>Aeshnidae</i> .         |
|    | { | Eyes more or less separated over dorsum of head; discoidal cells of fore and hindwings similar or dissimilar; female with or without zygopterous ovipositor. . . . .  | 3.                         |
| 3. | { | Middle lobe of labium with deep median fissure; eyes only moderately separated above; female with a zygopterous or pseudozygopterous ovipositor. . . . .  | 4.                         |
|    | { | Middle lobe of labium entire; eyes widely separated above; female without zygopterous ovipositor. . . . .   | <i>Gomphidae</i> .         |
| 4. | { | Pterostigma moderately long and slender; superior anal appendages of male narrow and acute at apex; female with a pseudozygopterous ovipositor. . . . .   | <i>Cordulegasteridae</i> . |
|    | { | Pterostigma enormously long and extremely slender; superior anal appendages of male broadly triangular, obtuse at apex; female with complete zygopterous ovipositor. . . . .  | <i>Petaluridae</i> .       |
| 5. | { | Primary antenodal nervures present but atrophied and inconspicuous; base of hindwing in male angulated; ear-shaped processes ( <i>auricles</i> ) on the sides of the 2nd abdominal segment of male; tibiae of male with keel-like armature; species nearly always metallic green or coppery metallic. . . . . | <i>Cordulidae</i> .        |
|    | { | Primary antenodal nervures always absent; base of hindwing in both sexes rounded; auricles never present; tibiae never armed with keels species rarely metallic. . . . .  | <i>Libellulidae</i> .      |

Superfamily AESHNOIDEA Tillyard emend.

Forms with the following archaic characters:—Eyes separated, zygopterous ovipositor fitted for inserting ova into plant tissues, larva with flat labial mask, setae absent (except in genus *Gynacantha* of the *Aeshnidae*), gizzard with more than a single tooth per fold. In the *Gomphidae* the eyes are separated but the ovipositor is not of the zygopterous type; in the *Aeshnidae* the eyes are confluent and the ovipositor is of the zygopterous type; lastly, in the *Petaluridae* the eyes are separated and the ovipositor is of the zygopterous type. It will be seen that such a distribution of characters is of a transitional nature, as the following formula shows:—

Family.	Eyes separated.	Zygopterous ovipositor.
<i>Gomphidae</i> . . . . .	+	—
<i>Petaluridae</i> . . . . .	+	+
<i>Aeshnidae</i> . . . . .	—	+

Other characters separating these three families will be found in the key given above.

Family I. GOMPHIDAE.

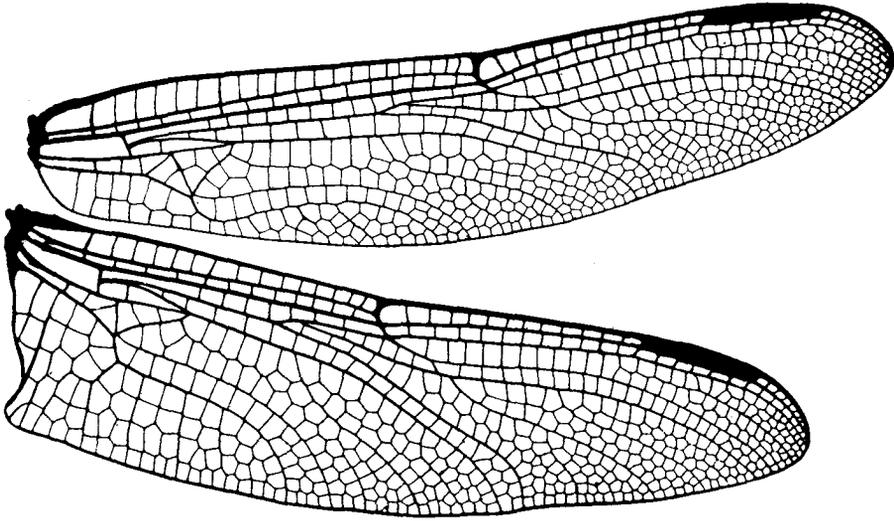


Fig. 7.—Wings of *Gomphidae* (*Ictinogomphus*), male.

The *Gomphidae* is a large family containing forms of clearly defined, homogeneous facies and all coloured black and yellow; sometimes one and sometimes the other colour preponderating. Generally those species confined to heavily forested areas are black marked sparingly with yellow, whilst those inhabiting more open country and desert zones, are yellow with more or less dark markings. The wings are always hyaline and uncoloured; the antenodal complex shows but a slight advance on that of *Heterophlebia*, the secondary veins being more numerous and present in both costal and subcostal spaces as in *Liassogomphus*. The base of the hindwing, in the male, is strongly angulated and excised, except in the more archaic genera; the discoidal cells are short and of different shape in the fore and hindwings, that of the latter being more elongated. At the base of each cell, another triangular cell appears for the first time—the “sub-triangle”, and posterior to this, although in a rudimentary condition, there may be a compact group of cells enclosed by the anal veins and known as the “anal-loop”. The head is transversely elongate as in the *Zygoptera* and the eyes are widely separated. The abdomen varies in shape in the genera, especially in regard to the end segments, the sides of which may be foliately dilated or elongated. The anal appendages of the male are highly specialized, the inferior being strongly bifid and its branches either

widely splayed or closely apposed and parallel. The female ovipositor is rudimentary and oviposition is accomplished by merely dipping the end of the abdomen in fast running water; the ova are swept off and sink to the bottom of the stream.

The larvae of this family are extremely variable, the body either elongated, fusiform and cylindrical or limpet-shaped or extremely depressed and dilated laterally. This polymorphism is an adaptation to their variable habitats, the fusiform cylindrical forms being adapted for burrowing deep in mud and sand; the depressed ones living at the bottoms of deep pools among leafy trash, where their form and dark blackish brown colouring renders them practically undifferentiated from their surroundings. The former types have the forelegs adapted for digging and the fore and mid-tarsi are only 2-jointed. The labium is of the flat, quadrate type, with narrow lateral lobes, rather obtuse at apex and fitted with a robust movable hook. The gizzard has 4 elongate folds furnished with a large number of undifferentiated teeth as in the *Zygoptera*.

The family is divided up into four subfamilies by venational differences but, generally, the range of these is remarkably small as compared to other Odonata, so that considerable difficulty has been met with in the classification of this family, and it may become necessary eventually to employ other characters for this purpose. Recently I have completed an examination of the penile organs of the whole of the genera of the *Gomphidae* and, although the results have been disappointing for classification purposes, they do not support the present classification by venational characters; thus the penile organs of the Epigomphine genera *Macro* and *Microgomphus* are quite similar to those of the Gomphine genus *Gomphus*, and the organs of the genera into which the latter genus has been split, viz., *Gomphurus*, *Lanthus* and *Stylurus* are all identical. On the other hand, species belonging to one genus such as *Anisogomphus* Selys, have the penes so entirely different, that it becomes a matter of surprise to find the venation so similar. The same may be said for the genus *Ictinogomphus* Cowley, which I have split up into several genera on the evidence of the penile organs; in these cases, however, there is some support from venational differences.

#### Key to the families of the *Gomphidae*.

- |    |   |   |
|----|---|---|
| 1. | { | Discoidal cell, hypertriangle and subtriangle all traversed by cross-veins. . . . . <i>Ictinogomphinae</i> .  |
|    |   | Discoidal cell, hypertriangle and subtriangle entire or only the discoidal cell traversed by a vein. . . . . 2.   |
| 2. | { | At least 3 or 4 cross-veins connecting MA to Rs in the hindwing; forking of Rs unsymmetrical. . . . . <i>Epigomphinae</i> .   |
|    |   | Only 2 (rarely 3) cross-veins connecting MA to Rs in the hindwing; forking of Rs symmetrical. . . . . 3.  |
| 3. | { | A supplementary longitudinal vein springing from the distal side of discoidal cell; this side of cell concave below origin of supplement; legs enormously long. . . . . <i>Hagentinae</i> . |
|    |   | No supplementary longitudinal vein arising from discoidal cell; legs short or of ordinary length. . . . . <i>Gomphinae</i> .  |

The New World forms of the *Ictinogomphinae* differ from those of the Old by possessing an incomplete basal antenodal vein in most or all of the

wings, and it may be necessary to separate these into a new subfamily under the name of the *Gomphoidiinae*.

Genera belonging to the *Gomphidae* by subfamilies are:—

*Gomphinae*: *Acrogomphus* Laid., *Africogomphus* Fras., *Agriogomphus* Selys, *Altaigomphus* Bart., *Anisogomphus* Selys, *Anormogomphus* Selys, *Archaeogomphus* Will., *Austrogomphus* Selys (Australian), *Burmagomphus* Will., *Cyanogomphus* Selys, *Cornigomphus* Mart., *Cyclogomphus* Selys, *Crenigomphus* Selys, *Davidius* Selys, *Davidioides* Fras., *Dromogomphus* Selys, *Erpetogomphus* Selys, *Gomphus* Leach, *Gomphurus* Need., *Hemigomphus* Selys, *Heterogomphus* Selys, *Ischnogomphus* Will., *Karschiogomphus* Shout., *Lanthus* Need., *Labrogomphus* Need., *Lamelligomphus* Fras., *Lestinigomphus* Mart., *Libyogomphus* Fras., *Megalogomphus* Camp., *Merogomphus* Mart., *Nepogomphus* Fras., *Notogomphus* Selys, *Nihonogomphus* Oguma, *Onychogomphus* Selys, *Octogomphus* Selys, *Oxygomphus* Lacroix, *Ophiogomphus* Selys, *Paragomphus* Cowley, *Platygomphus* Selys, *Perissogomphus* Laid., *Podogomphus* Selys, *Stylogomphus* Fras., *Stylurus* Need., *Phyllogomphus* Selys, *Trigomphus* Bart., *Tragogomphus* Sjos., *Neogomphus* Selys, and *Neurogomphus* Karsch.

*Epigomphinae*: *Epigomphus* Selys, *Heliogomphus* Laid., *Leptogomphus* Selys, *Macrogomphus* Selys, and *Microgomphus* Selys.

*Ictinogomphinae*: *Austrictinogomphus* nov. gen., *Cacoides* Cowley, *Diphlebia* Selys, *Diastatomma* Selys, *Desmogomphus* Will., *Gomphidia* Selys, *Ictinogomphus* Cowley, *Indictinogomphus* Fras., (Oriental and Australian), *Lindenia* Vanderl., *Negomphoides* Muttow., *Sinictinogomphus* Fras., *Zonophora* Selys.

*Hageninae*: *Hagenius* Selys, *Sieboldius* Selys.

Fossil genera: *Nannogomphus* Handl., *Protolindenia* Deichmüller, *Necrogomphus* Camp., and *Phengothemis* Handl. (all Jurassic). *Gomphus*, *Gomphoides* and *Ictinogomphus* have also been reported from Bavarian amber and the Miocene.

Only two genera are found in Australia, *Ictinogomphus* and *Austrogomphus*, the latter exhibiting such a high degree of specialisation of the genitalia that it must have been isolated from the rest of the family over a vast period.

#### Family PETALURIDAE Tillyard. (Fig. 8.)

The Petaluridae is the smallest family of the suborder *Anisoptera* and contains only nine species belonging to five genera. Species belonging to this family are the giants of present-day Odonata, one Australian form being the largest dragonfly known. They are the remnants of a once

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The genus *Austrictinogomphus* is raised here to include a single species—*Ictinus acutus* Laidlaw, which differs from all other species of genus *Ictinogomphus* (= *Ictinus* nom. preoc.) by the superior anal appendages forcipated, inferior appendage with its long fine branches widely divaricate, and, lastly, by the shape of the penile organ which is entirely different from that of any other in the genus.

flourishing and widespread fauna as is evidenced by their broken distribution throughout the world.

The wings are long, narrow, subfalcate and densely reticulated and, as in the *Gomphidae*, they are always hyaline and uncoloured; the antenodal complex is similar to this last family; the base of the hindwing is strongly angulated and excised; the discoidal cells are usually similar in the fore and hindwings, but in *Phenes* and *Tachopteryx*, that of the hindwing is smaller and more oblique; a subtrigone is present in the forewing and is usually divided into 2 or more cells; the anal-loop is small and rudimentary, being usually open posteriorly and made up of not more than 3 to 5 cells; the pterostigma is of enormous length and extremely narrow and

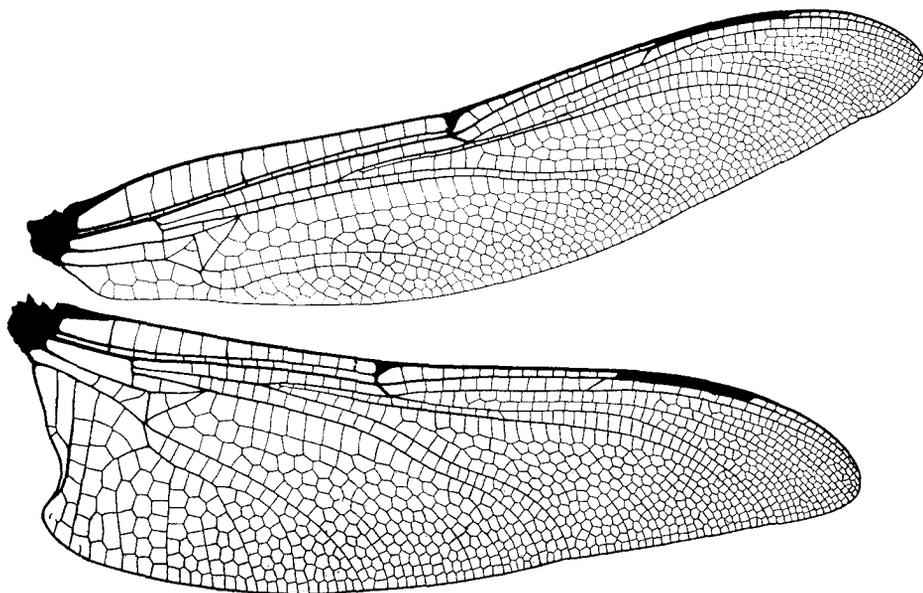


Fig. 8.—Wings of *Petaluridae* (*Uropetala*), male.

is often separated from its brace which lies some distance proximally, especially in *Phenes*. (This feature is not archaic as generally supposed, since the pterostigma is absent in the *Protodonata* and either short or very broad in the earliest known fossil *Odonata*.) The proximal position of the brace suggests that the pterostigma was much longer at one time than it is at present in these forms. The head is massive and the eyes widely separated as in the *Gomphidae*; the abdomen is elongate and cylindrical, with, in some genera, in the female, the end segments deflected dorsalwards so that the zygoterous type of ovipositor comes to look directly posteriorwards in these. The anal appendages are highly specialized, the superiors more or less broadly foliate or triangular except in *Phenes*, and the inferior hastiform or elongate and hook-like.

The larvae, which are best known from Dr. Tillyard's researches on the Australian forms, but also from the N. American *Tachopteryx thoreyi*, are quite the most interesting of the whole order *Odonata*, from their

unique habit of living and burrowing in peaty or marshy soil, into which they may penetrate to a depth of a foot or more, emerging only during the night to seek their prey. The presence of vestigial spiracles in the larvae of all *Odonata*, indicates that this mode of living was, at one time, common to the whole order, so that the *Petaluridae* must be regarded as very archaic; it can be regarded as improbable that the habit has been re-acquired. The larvae are curious grub-like creatures, with soft, whitish elongate body, long spidery legs and flat type of labium found in the *Zygoptera*, but differing from that of the *Gomphidae* by being slightly concave and considerably broadened; the gizzard is of archaic structure in that it is furnished with 8 folds, as in the higher *Zygoptera*, and with small, undifferentiated teeth.

In my monograph on this family in 1932, I divided it up into two sub-families, but, it must be confessed, on rather slender grounds. Reviewing the *Petaluridae* again, after a lapse of some eight years, I still adhere however to this classification but further restrict the subfamily *Tachopteryginae* to the genus *Tanypteryx*; the name of the subfamily must therefore be changed to *Tanypteryginae*. I do this because, with the whole of the species in review, one cannot help noticing the smaller size and the boldly contrasted colouring of the two species of *Tanypteryx* as contrasted with the huge size and ill-defined, dowdy colouring of the rest of the species belonging to the family; there are also venational differences which are noted in the key below.

Key to the subfamilies of the *Petaluridae*.

- Species coloured brown or blackish brown, with poorly contrasted and ill-defined markings of yellow; primary antenodal nervures separated by not less than 4 or 5 secondaries in fore and hindwings. . . *Petalurinae*.  
 Species coloured black and yellow with strongly contrasted, well-defined markings as in the *Gomphidae*; primary antenodal nervures separated by only 3 secondaries in the forewing and by only 2 in the hind. . . . .  
 . . . . . *Tanypteryginae*.

Two out of the five known genera and more than half the species are found in Australia and New Zealand. The genera according to subfamilies are:—

*Petalurinae*: *Petalura* Leach (Australia), *Uropetala* Selys (New Zealand), *Phenes* Rambur (S. America), *Tachopteryx* Selys (N. America). *Tanypteryginae*: *Tanypteryx* Kennedy (N. America and Japan. Fossil genera: *Mesuropetala* Handl., (Jurassic), *Libellulum* West., (= *Cymatophlebia* Handl., (Jurassic).

Family AESHNIDAE. (Figs. 9 & 10.)

Insects of large size and robust build, characterised by the large globular head made up in great part by the enormous eyes which are broadly confluent across the middle line of the head. The vesicle is crowded forward and the occiput reduced to a tiny triangular area; the wings are elongate, closely reticulated, hyaline and nearly always uncoloured; the antenodal complex not differing from that of the *Gomphidae*, but in some genera, accessory basal antenodals are found proximal to the primaries, and these are often associated with cross-veins in the median space; the discoidal cells are closely similar in shape in fore and hindwings, and are usually divided up into two or more cells; the anal-loop always present and differing somewhat in shape in the genera, usually subquadrate; pterostigma

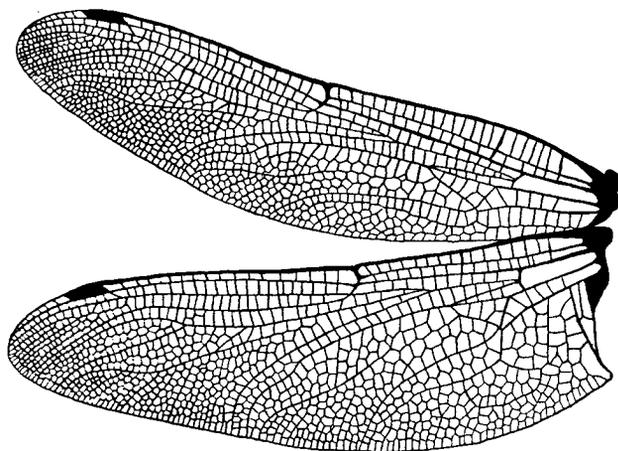


Fig. 9.—Wings of *Aeshnidae* (*Aeshna*). Note oblique veins joining Riv + v and MA.

variable, usually elongate and narrow, braced or not; thorax robust; legs short and robust; abdomen long and cylindrical, with or without lateral ridges on segments 3 to 8; anal appendages very variable, the inferior usually narrowly triangular but, in some genera, broad and more or less emarginate at apical end. Female ovipositor of the archaic zygopterous type, and formed for inserting ova into plant tissues; of variable shape and length and usually furnished with accessory organs or a "genital plate", the function of which is to fix the end of the abdomen whilst the ova are being inserted.

The larvae, which live in weed or crawl on the surface of mud and trash, are very similar in appearance in the genera. Head and eyes broad and flattened; labium of the flat type but very elongate and triangular in shape; lateral lobe of the Gomphine shape but obtuse at apex and furnished here with a robust, inwardly directed spine; setae absent except in the sub-family *Gynacanthaginae*. The gizzard has four folds, each furnished with a few, closely-set teeth approaching the form of a molar.

This family divides naturally into two large sections by the character of the two main veins Riv + v and MA. In the first section, *Aeshnidi*, the vein MA converges on Riv + v and shortly after the level of the nodus, at a point where it begins to turn posteriorwards, it weakens or atrophies or, more usually, is attached to the latter vein by a short oblique cross-vein. At this point, the distal portion of the vein MA shows a distinct bulging away from Riv + v, after which it returns to and runs parallel to that vein. Various degrees of this formation may be found throughout the family, but it reaches its perfection in the genus *Anaciaeshna*. In the second section, *Brachytridi*, there is no sign of this formation, or, at the most, but a slight local curvature of MA; the oblique vein is never present.

#### Section BRACHYTRIDI.

The veins Riv + v and MA running in an unbroken curve and parallel to one another to the wing border or slightly divergent at the distal ends.

The section is divided into three subfamilies by venational and other characters, the principal one of which is the vein IRiii, which may be simple and unbranched or symmetrically forked from a point more or less proximal to the level of the pterostigma.

Key to the subfamilies of the *Brachytridi*.

- The vein IRiii simple and unforked. . . . . 2.  
 The vein IRiii symmetrically forked. . . . . *Brachytrinae*.  
 A chain of reddish spots along the costal border of all wings; anal-loop absent. . . . . *Neopetalinae*.  
 Costal border unspotted; anal-loop present. . . . . *Gomphaeshninae*.

Subfamily GOMPHAESHNINAE nov. subfam.

Forms belonging to this subfamily, in addition to the simple unforked condition of IRiii, generally show but a flat curvature of Riii towards the pterostigma, a small anal-loop, a discoidal field beginning with only 2 rows of cells, only 1 or 2 rows of cells between IRiii and the radial supplement (Rspl) and between MA and the median supplement (Mspl), and finally, the discoidal cell of hindwing broader than that of the forewing. Genera are: *Boyeria* MacLach., *Oligoaeshna* Selys, *Allopetalia* Selys, *Gomphaeshna* Selys, *Linaeshna* Mart., *Basiaeshna* Selys, and *Hoploaeshna* Karsch. There are no Australian genera.

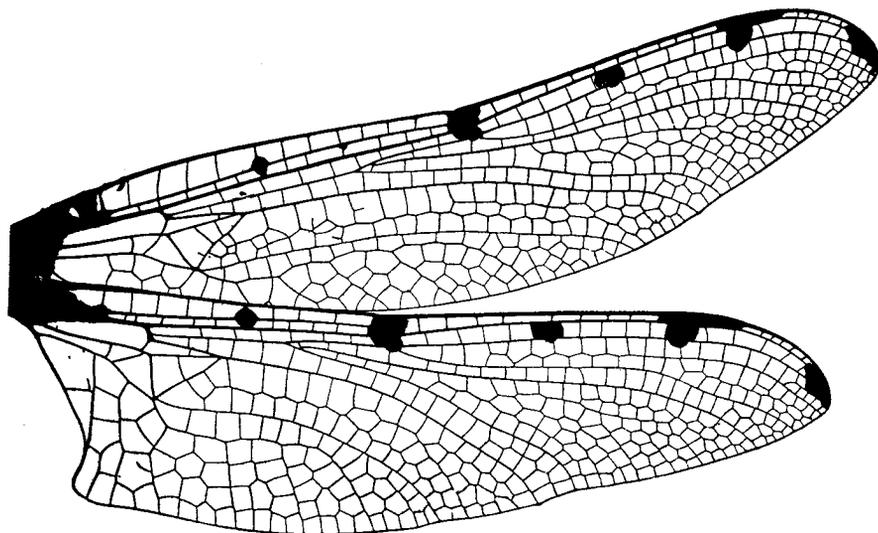


Fig. 10.—Wings of *Neopetalinae* (*Austropetalia patricia* Tillyard), male.

Subfamily NEOPETALINAE nov. subfam. (Fig. 10.)

This subfamily consists of a small group of monotypic genera characterized by inferior anal appendages of the male trifold at apex and by the costal border of all wings decorated by a chain of ruby-red spots (these are situated at the base, midway between the base and nodus, at the nodus, midway between the latter and the pterostigma, at the pterostigma and apex of wing). The discoidal cells are of the same size and shape and

traversed by a single vein; Rspl is rarely present and Mspl never so; anal-loop absent; IRiii simple and unforked; Riv + v and MA usually diverging towards the wing border; lastly the pterostigmal brace is situated at its middle instead of at the proximal end as in other Aeshnines.

Apart from the remarkable colour scheme of the costal border, the most interesting fact about this small subfamily is its limited distribution to Australasia and S. America. Such a distribution is clearly not a recent occurrence and can only have been achieved when these two countries formed part of a continuous Antarctic continent. This indicates the *Neopetalinae* as of very archaic origin and gives an added importance to their venational characters, since in them, we have a means to estimate the age of other Aeshnines. These characters are: presence or absence of Rspl and Mspl, forked or unforked IRiii, and presence or absence and the relative size of the anal-loop. Eyes separated or just meeting.

Genera are: *Austropetalia* Till., (Australia), *Archipetalia* Till., (Tasmania), *Neopetalia* Cowley, *Hypopetalia* MacLach., and *Phyllopetalia* Selys (all S. America).

#### Subfamily BRACHYIRINAE nov. subfam.

This large subfamily contains two well-defined groups and a small number of specialized forms which appear to be rather isolated from the rest. One group, the Australian, has the median space free of cross-veins, whilst the other, the Oriental, has the same space traversed by a number of veinlets. In this latter group, the arculus is often situated more distally than in other Aeshnines and usually lies at a level midway between the two primary antenodals or, in some, at the level of or even distal to the outer primary (*Petaliaeshna* Fraser and *Periaeshna* Mart.). Also the female genitalia more nearly approaches the form of the archaic zygopterous organs.

Of the isolated forms, *Austrophlebia* Till., is of enormous size, and nearly equals in this respect, *Petalura ingentissima* Till., another Australian form; its wings are bordered with dark brown along the costa, a cryptic device which harmonizes perfectly with the undersides of tree-fern fronds on which the insect prefers to take its rest. *Telephlebia* Selys, another Australian genus, is remarkable for its rich venation, quite unique in recent *Aeshnoidea*. In it, the space basal to the primary antenodals is filled with coinciding accessory antenodals, as in the higher forms of the *Zygoptera* and *Anisoptera*. With such a formation, we should expect to find the primary antenodals atrophic, but they are still present; it is the one exception which proves the rule. Another rare character is found in this genus, viz., the prolongation of the subcostal vein through and beyond the nodus. This character is also found in two other Aeshnines, the Japanese genus *Aeshnophlebia* Selys, and the Indian genus *Indophlebia* Fraser, although the three are not nearly related. It has been regarded as an archaic character inherited from the ancient Carboniferous *Odonata*, but a little reflection will show that this is a secondary acquirement, since the phylogeny of the Order excludes such a wild theory.

The genera are: (1) Median space free—*Austroaeshna* Selys, *Notoaeshna* Till., *Austrophlebia* Till., (all Australia), *Planaeshna* MacLach., *Aeshnophlebia* Selys (Japan), *Tetracanthagyna* Selys (Oriental), *Epiaeshna* Hagen, *Nasiaeshna* Selys (America), and *Brachytron* Evans (Europe). (2) Median space crossed—*Dendroaeshna* Till., *Telephlebia* Selys (Australia), *Cepha-*

*laeshna* Selys, *Periaeshna* Mart., *Petaliaeshna* Fraser, *Gynacanthaeshna* Fraser, *Indophlebia* Fraser (Oriental), and *Caliaeshna* Selys (Central Asia).

#### Section AESHNIDI.

The veins Riv + v and MA gradually converging and either fusing or connected by an oblique vein; MA atrophied at its distal end. This section, which is the dominant one of the *Aeshnidea*, falls naturally into four sub-families on characters given in the following key:—

#### Key to subfamilies of the *Aeshnidi*.

- |    |   |   |
|----|---|---|
| 1. | } | Hindwing rounded at the base in both sexes; no oreillets on the sides of segment 2; Riii making an abrupt bend towards the pterostigma; anal triangle absent. . . . . <i>Anactinae</i> .        |
|    |   | Hindwing angulated and excavated at base in the male; oreillets present on sides of segment 2; Riii not usually making a bend towards the pterostigma; anal triangle always present. . . . . 2. |
| 2. | } | Female genitalia with simple rounded, finely spined dentigerous plate. . . . . <i>Aeshninae</i> .   |
|    |   | Female genitalia with dentigerous plate produced into two long robust spines. . . . . <i>Gynacanthaginae</i> .  |
|    |   | Female genitalia with dentigerous plate produced and ending in 4 or more robust spines. . . . . <i>Polycanthaginae</i> .  |

#### Subfamily AESHNINAE. (Fig. 9.)

Forms belonging to this subfamily are the most widely distributed and dominant of all the Aeshnines. Their characters are those of the family: MA fused with Riv + v near its distal end; discoidal cells elongate, narrow, of similar shape and size in fore and hindwing; discoidal field beginning with 3 rows of cells; arculus lying at a level much nearer to the proximal primary antenodal; median space entire; subtrigones weak or absent; Rspl and Mspl markedly curved and enclosing between themselves and IRiii and MA respectively 4 or more rows of cells; anal triangle variable, or 2 or 3 cells, narrow or broad; membrane large; pterostigma narrow, of variable length, always braced; IRiii forked shortly before the level of pterostigma. Eyes broadly confluent; abdomen long, cylindrical; anal appendages variable, the inferior usually triangular with acute apex; female dentigerous plate rounded, not produced, coated with numerous fine spines. The subfamily contains only one genus—*Aeshna* Fabr., which is distributed over the whole of northern Asia, Europe and North America. A few species have extended into the montane areas of Central Africa, and others far into S. America. The most remarkable fact, however, concerning the distribution, is the occurrence of a single, typical species in Australia—*A. brevistyla*. The origin of this species and its entire isolation from all other species of a dominant genus is an insoluble problem. *Subaeshna* Mart., (S. America), probably belongs to this subfamily.

#### Subfamily ANACTINAE nov. subfam.

Very large and very robust dragonflies with characters similar to the last subfamily but with the hindwing rounded in both sexes, except in genus *Anaciaeshna* which is an annectant between this subfamily and the *Aeshninae*. The oblique vein connecting MA with Riv + v is much better defined in these forms and there is a distinct break in or actual loss of the distal end of MA. In consequence of the rounded nature of the base

of the hindwing, the anal triangle is absent, as also are the oreillets on the sides of segment 2. These latter organs are only present in species with the base of the hindwing notched and it has been thought that they play some part in flight; this is not correct, however, their function being accessories to the genitalia. The deep notch on their hinder border and the imbricated spines on this same border arrest the end of the female abdomen when seeking for the male genital fossa which lies between the oreillets; they are, in fact, a guide to the female during this act. In genera belonging to this subfamily and others with rounded base to wings, other organs are found which have taken over the function of the oreillets, so that the latter have atrophied or disappeared. The abdomen of the male is furnished with supplementary ridges on segments 4 to 8, which are vestigial in *Anaciaeshna* and absent on segment 8, and again in *Oreaeshna*, where they are present only on segments 7 and 8; the anal appendages are not unlike many in the *Aeshninae* but the inferior is usually shorter and obtuse at apex; the female genital plate is quite similar to the *Aeshninae*.

Genera are: *Anax* Leach (*A. guttatus* Burm., is found in Australia), *Hemianax* Selys (*H. papuensis* Burm., is found in Australia). The former genus extends right round the world, both in temperate and tropical zones; the latter extends from Europe to Australia. *Anaciaeshna* Selys (Tropics of the Old World), *Oreaeshna* Lieft., (New Guinea; an annectant form combining the characters of *Anaciaeshna* and *Aeshna*).

#### Subfamily GYNACANTHAGINAE.

The forms in this large subfamily are remarkably homogeneous in form and colouring and considerable difficulty is often met with in the determination of species; all, with but few exceptions, are crepuscular in habit and all oviposit in dry soil, a circumstance which has led to the evolution of a highly specialized form of ovipositor. The eyes are very large and very broadly confluent; the anal appendages long and thin in both sexes (because of this formation and because of the peculiar nature of oviposition, the appendages of the adult female are nearly always found broken off at the base). The genital plate is produced into a robust two-pronged fork which is employed for digging during oviposition; it is closely similar to that of *Periaeshna* and *Gynacanthaeshna* of the subfamily *Brachytrinae*. Dr. Laidlaw (Proc. U.S. Nat. Mus., 62:3) commenting on this similarity in genera belonging to two different subfamilies is at a loss to know whether we are dealing with a parallel development in venation or genitalia; I think that there can be no doubt that the parallelism is in the evolution of the genitalia, for if we remember that all those species which oviposit in dry earth have such organs, it will be seen that similar habits have called forth similar eclectic organization. The finely spined organ of the *Aeshninae* would soon become clogged with soil if employed for digging, but the pronged fork of the *Gynacantha* is admirable for such a purpose. The venation of these forms is very similar to that of the *Aeshninae*, but the reticulation is much closer and there is a corresponding increase in the number of cell rows between the Radial and Medial supplements and opposing sectors.

Genera are: *Gynacantha* Rambur (Circumtropical, including Australia), *Austrogynacantha* Tillyard (Australia), *Plattycantha* Martin (Papua), *Cornacantha* Martin (Papua), *Heliaeshna* Selys (Oriental and Ethiopian), *Triacanthagyna* Selys (Central and South America), *Neuraeshna* Selys (South America), *Staurophlebia* Brauer (S. America). The last two genera

resemble *Aeshnophlebia* and *Telephlebia* in having the subcostal vein prolonged through and beyond the nodus, but it is merely another case of parallel development.

Subfamily POLYCANTHAGINAE nov. subfam.

This small subfamily is formed to include a few aberrant forms closely related to the *Aeshninae*. They resemble that subfamily in venation, but the females show a high specialization in their colour and in the formation of their genitalia. The latter has the dentigerous plate prolonged backwards and ending in several robust spines and is employed for digging as in the *Gynacanthaginae*. Unlike this subfamily, species are diurnal in habits, which may account for the bright heliochromatic colouring of the females. There is only one genus, *Polycanthagyna* Fras., (Oriental and Japan).

Fossil genera: In the Tertiary deposits, more especially in the Miocene of Germany, Russia and N. America, a number of genera belonging to the *Aeshnidae* have been described. Of these, Needham is of opinion that only one, *Aeshna solida* Say (Florissant, Miocene), can be considered as belonging to *Aeshna* sens. strict., whilst the others have been placed in recent genera, *Basiaeshna*, *Hoploaeshna*, or accommodated in new ones, *Morbaeshna* Need., *Lithaeshna* Cock., *Projagoria* Martyn., *Epacantha* Martyn., *Necracantha* Martyn., and *Triaeshna* Champion. Of all these, *Hoploaeshna separata* (Scud) (Miocene, Florissant), is the only one I can find in which MA is defective distally, and so lies within the section *Aeshnidi*; all the others belong to the section *Brachytridi* and to either of the subfamilies *Brachytrinae* or *Gomphaeshninae*.

We are now in a position to discuss the probable ages of the various units which make up the family *Aeshnidae*. Among recent forms, the Neopetalinae appear to be the most archaic, since in them the anal-loop is absent, Rspl and Mspl are elementary or absent, MA is unbroken distally and IRiii is unforked. Lastly, the eyes are separated or only just meet. All these characters agree with those of the mesozoic forms and, so, we can say with certainty that the *Brachytridi* preceded the *Aeshnidi*, and, of the former, the *Gomphaeshninae* preceded the *Brachytrinae*. From the general venation, one would conjecture that the *Aeshnidae* arose from the ancient Petalurine stem; they are at least as old, and probably older than the *Cordulegasteridae*, as the zygoterous type of ovipositor and the more primitive type of larva seem to indicate.

Superfamily CORDULEGASTEROIDEA.

The *Cordulegasteroidea* include the three remaining families of the Anisoptera—*Cordulegasteridae*, *Cordulidae* and *Libellulidae*. Apart from ordinal characters and the absence of a typical zygoterous ovipositor, no common character exists in the imagines, by which close relationships may

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The name "*Aeshna*" was emended in Illiger to "*Aeschna*", but has since been restored to its original spelling. Following on this, in this paper, I have emended all the hyphenated names founded on the latter; the International Rules for Nomenclature do not provide for such a contingency, but it seems logical that if a wrongly spelt basic name is emended, then all those founded on the mis-spelt name ought to be so too. *Oploaeshna* Selys is here replaced by *Hoploaeshna* Karsch; *Oploaeshna* was only proposed by Selys and later validated by Karsch, who emended the spelling.

be demonstrated, and it is on the evidence of larval characters that we rely for establishing these. These characters are:—Labium deeply concave and fitting over the face like a gas-mask, plentifully furnished with setae, both on mentum and lateral lobes; the latter with apposed borders biserrate, serrate or crenate; movable hook small and reduced; gizzard with four folds, each fold furnished with a single robust tooth.

Family 1. CORDULEGASTERIDAE. (Figs. 11 & 12.)

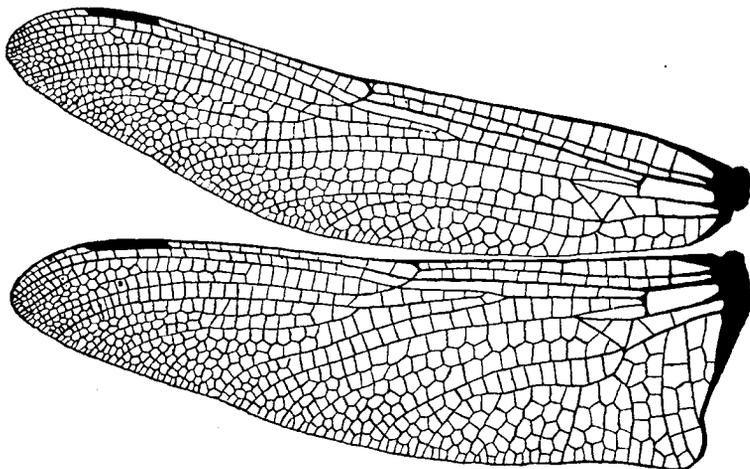


Fig. 11.—Wings of *Cordulegasteridae* (*Cordulegaster annulatus* Latr.), male.

This family contains two large groups of dragonflies which vary so much in facies and detail, that until a few years ago they were considered as not being at all closely related, and it was only the discovery of the larva and an examination of its characters which proved beyond doubt the place of the *Chlorogomphinae* in the family *Cordulegasteridae*. The insects contained in these two groups agree in being of large and robust size, with head transverse and eyes more or less separated, although not to the same extent as in the *Gomphidae*. The larvae, on the other hand, are so closely similar that they are difficult to separate; the body is long and fusiform, tapering towards the end of abdomen; labial mask of the concave or "spoon" shape, with broad triangular, cupped lateral lobes, furnished with setae and a longish movable hook, and with the apposed margins deeply serrate and biserrate. This latter feature is of great importance, since we find it repeated in the following two families, *Corduliidae* and *Libellulidae*. The head is robust and armed with a projecting frontal plate, which it apparently employs for burrowing in sand; legs moderately long and not specialized for digging as in the *Gomphidae*; gizzard highly specialized, made up of 4 folds, each of which is furnished with a single robust tooth more or less spined on its free border. This type of gizzard is repeated in the same two families mentioned above, indicating the closest relationship between them and the *Cordulegasteridae*. The family contains two recent and one fossilerous subfamily.

Key to the subfamilies of the *Cordulegasteridae*.

- Wings similar in the sexes, occasionally coloured at the base in the female; discoidal cells similar in shape and size in fore and hindwings; anal-loop rudimentary; tibiae without keels; ovipositor of great length. . . . . *Cordulegasterinae*.
- Wings usually variable in the sexes and usually more or less coloured and with the base of hindwing greatly broadened in the female; discoidal cells of variable shape and size in fore and hindwings, especially in the female; anal-loop well developed; tibiae of male with keels; ovipositor short, inconspicuous. . . . . *Chlorogomphinae*.
- Fossil species with rather broad wings and with extraordinary closely reticulated venation; discoidal cells differing in shape and size in fore and hindwings; ovipositor of great length as in the . . . . .  
. . . . . *Cordulegasterinae* .. *Aeshnidinae*.

## 1. Subfamily CORDULEGASTERINAE. (Fig. 11.)

Forms belonging to this subfamily are distinguished by the great length of the ovipositor of the female, a condition due to hypertrophy of the terebra, the valves, which they conceal, being minute and rudimentary; the eyes are more widely separated than in the following subfamily; the discoidal cells are similar in the wings and elongated in the length of the wing and divided by a cross-vein; Rspl is well-defined in its basal part only, and Mspl is altogether absent, as also is the anal-loop; the pterostigma is narrow and usually elongate; the antenodal complex is similar to that of the *Gomphidae*, basal antenodals being absent; the median space is always free of veins. Abdomen cylindrical, somewhat dilated in the end segments, and always longer than the wings. Only in the females of the genus *Anotogaster* do we find any trace of colouring, although very adult females of *Neallogaster* may be more or less deeply infumated. The tibiae of the males are never keeled. Larvae as for the family.

Genera are: *Cordulegaster* Leach (Palaeartic, Nearctic, Oriental and one species from the Andes, S. America), *Anotogaster* Selys (Oriental, China and Japan), *Neallogaster* Cowley (Oriental). There are no Australian species.

## 2. Subfamily CHLOROGOMPHINAE.

There is only one genus in this family, which is distinguished by the short ovipositor of the female; the eyes are separated to a less degree than in the *Cordulegasterinae*, and, in the males, may be just in contact; the discoidal cells are dissimilar in the wings, that of the forewing similar to the *Cordulegasterine*, that of the hindwing elongate in the breadth of the wing, especially in the females, and divided into 3 or 4 cells; the antenodal complex is always reinforced by one or more accessory basal veins and the median space is traversed by one or more cross-veins; the anal-loop is usually highly developed and may consist of a great number of cells; Rspl and Mspl are generally absent. Abdomen cylindrical or rather compressed in the females, shorter or much longer than the wings. In the males, the apices are nearly always tipped with black, and in the females the whole wing may be tinted with amber or even opaque in parts. The tibiae of the males are invariably keeled, as in the following family, *Corduliidae*.

Genera are: *Chlorogomphus* Selys (Oriental and extending to Formosa, the Philippines and the Sondaic Islands). A second genus was erected by

Selys, *Orogomphus*, but it is doubtful if it can be separated from *Chlorogomphus* by any individual characters. There are no Australian species.

### 3. Subfamily AESHNIDIINAE. (Fig. 12.)

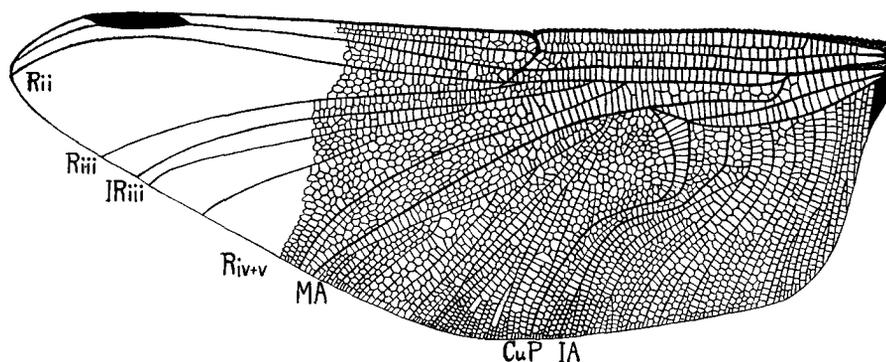


Fig. 12.—Wings of *Aeshnidiinae* (*Aeshnidiopsis flindersiensis* Wood).

This subfamily is erected to contain three fossil genera which are characterized by possessing a long ovipositor similar to that of the *Cordulegasterinae*; the eyes are more widely separated than in this subfamily and the discoidal cells vary in the wings as in the *Chlorogomphinae*. The wings are said to possess a subtrigone, but it is evident from its formation that it is not the same triangle common to the *Aeshnidae*, and, in most cases, is open posteriorly. The reticulation is very close in at least two of the genera; in the Australian form *Aeshnidiopsis* Tillyard, the venation is so close that there are two rows of cells between the costa and subcosta and a sector intercalated between these two main veins; only in the Australian genus *Telephlebia* do we find anything approaching such a condition. The three genera forming the subfamily have been placed in the *Aeshnidae* but because of the *Cordulegasterine* ovipositor, as well as the widely separated eyes, I have transferred them to the present family.

Genera are: *Aeshnidium* West., *Urogomphus* Handl., and *Aeshnidiopsis* Tillyard (Upper Jurassic and Cretaceous), the latter from Queensland Cretaceous. Tillyard (*Biology of Dragonflies*) states:—"The *Aeshnidiinae* seem to have died out in Cretaceous times; unless, indeed, the recent *Chlorogomphus* be a close ally or a descendant from them". I think that they are to be regarded as an annectant group between the two recent subfamilies of which they share the characters about evenly balanced. If so, then the *Chlorogomphinae* are the most recent forms in this complex, which may explain their comparative isolation within well-defined boundaries.

#### Superfamily LIBELLULOIDEA.

Generally, forms belonging to this superfamily are the most dominant and the most highly developed venationally of the whole order Odonata. The wings are hyaline, usually uncoloured, but in some genera are partly coloured and opaque; the hindwing is much broader at the base than the forewing and rounded or angulated in the male, always rounded in the female. Except in the most archaic forms, the antenodal complex has attained its completion, the primaries are absent or very poorly developed

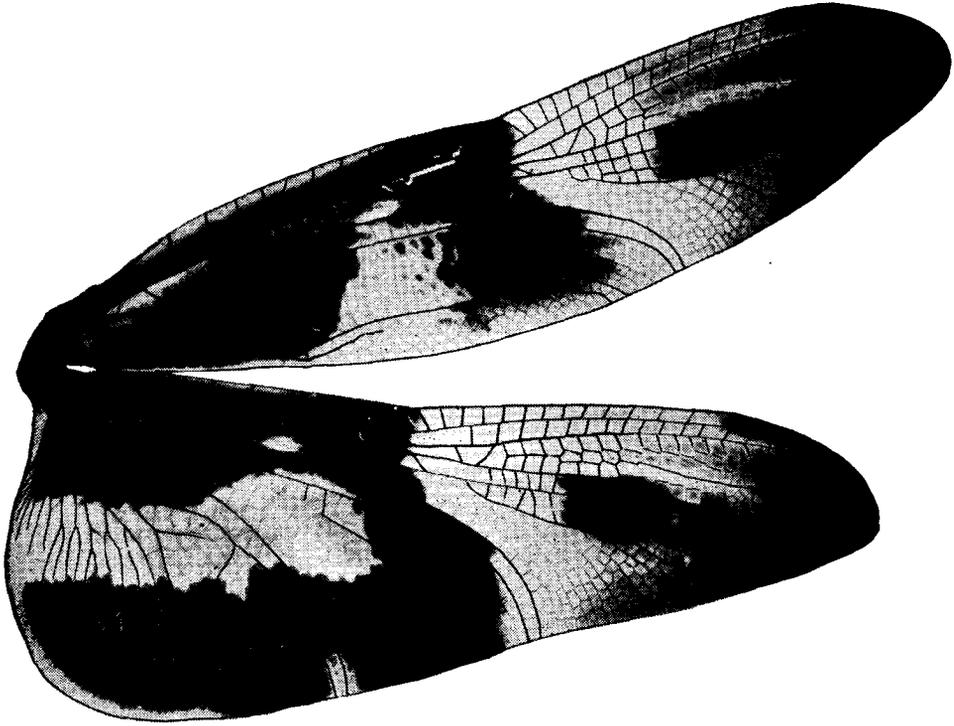


Fig. 13.—Wings of *Libellulidae* (*Rhyothemis regia regia* Brauer), male.

and the secondary costal and subcostal antenodals are all strictly aligned to one another. The discoidal cell varies in shape and position in the fore and hindwing; in the former it is always situated far distal to the level of the arculus, whilst in the latter it may lie distal or be recessed entirely to the level of the arculus; anal-loop absent or present, rudimentary or developed as a long, stocking-shaped formation in the base of the hindwing; *Rspl* and *Mspl* usually present, running parallel or concave to *IRiii* and *MA* respectively; pterostigma always present and of Lestine shape. Head globular, eyes rounded and either just meeting dorsally or broadly confluent; labrum with very small unclleft median lobe, largely overlapped by broad lateral lobes; thorax robust; abdomen of very variable shape, cylindrical or carinated, depressed or compressed, fusiform or tapering analwards, as long as, but usually shorter than the wings. Anal appendages of male of simple design, but more highly specialized and intricate in some genera. Female without a conspicuous ovipositor (except in a few aberrant species), both terebra and valves atrophied; oviposition accomplished by merely dipping the end of abdomen in water.

Larvae variable in the subfamilies but all alike in possessing a deeply cupped or spoon-shaped labium, the lateral lobes of which are either serrate in the archaic forms, or more or less deeply crenate along the inner border

in others; larval gizzard possessing 4 folds, each furnished with a single robust tooth. In these two characters, we find a strong connection between the *Libelluloidea* and the *Cordulegasteridae*.

Key to the families of the *Libelluloidea*.

- Tibiae of males with a long, lamina-shaped keel on the flexor surface; base of hindwing in males strongly angulated (except in genera *Hemicordulia* and *Procordulia*); oreillets present on the sides of segment 2; body usually coloured metallic. . . . . *Corduliidae*.
- Tibiae of males without keels; base of hindwing in both sexes rounded; oreillets absent on segment 2; body rarely coloured metallic. . . . . *Libellulidae*.

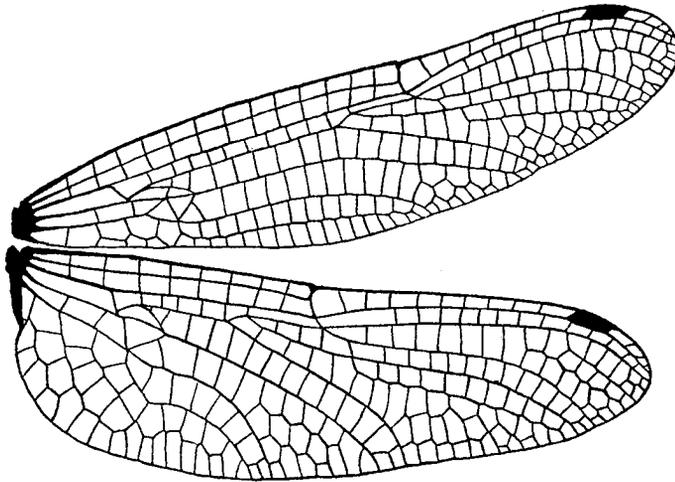


Fig. 14.—Wings of *Corduliidae* (*Idionyx saffronata* Fraser), male.

Family CORDULIDAE.

Dragonflies of large or medium size, with hyaline, uncoloured wings (very rarely coloured in part), angulated at the base in the males (except in genera *Hemicordulia* Selys and *Procordulia* Mart), nodus situated distal to middle of costa (very far so in *Idionyx*), pterostigma variable, usually rather short; anal-loop rarely absent, but vestigial in some genera and compact or elongated in others; antenodal complex graduating from an incomplete, Gomphine-like one in the archaic forms, to a complete or nearly complete one in the higher forms; the primaries, even in the higher forms, are still discernible although greatly atrophied; Rspl usually present but Mspl more often absent; anal triangle present in all males save those with rounded base to hindwings. Body colouring almost invariably partly or wholly metallic; abdomen cylindrical in the males or somewhat expanded analwards, usually compressed in the females. Larvae as variable as the imago; three types are known and are described below under the sub-families.

Key to the subfamilies of the *Corduliidae*.

1. { Discoidal cell with costal side broken in all wings; anal-loop absent; hindwing not markedly broader than the forewing. . . . . *Cordulephyinae*.  
 Discoidal cell with costal side broken in all wings; anal-loop present, elongate; base of hindwing enormously expanded, much broader than forewing. . . . . *Neophyinae*.  
 Discoidal cell with costal side straight, unbroken; anal-loop usually present, more or less well-defined. . . . . 2.
2. { Anal-loop absent or rudimentary and with its midrib zigzagged between cells. . . . . *Gomphomacromiinae*.  
 Anal-loop well-defined, its midrib, when present, running unbrokenly between cells or slightly zigzagged. . . . . 3.
3. { Sectors of arculus fused for a long distance in all wings; anal-loop elongate, its midrib slightly zigzagged between cells; discoidal cell in hindwing incompletely recessed to arculus. . . . . *Idionychinae*.  
 Sectors of arculus divaricate from origin in all wings; anal-loop elongate, its midrib not zigzagged between cells; discoidal cell completely recessed to arculus. . . . . *Corduliinae*.  
 Sectors of arculus divaricate from origin in forewing, slightly fused in the hindwing; anal-loop compact, without midrib; discoidal cell in hindwing not recessed to arculus. . . . . 4.  
 Sectors of arculus divaricate from origin in all wings; anal-loop elongate, its midrib not zigzagged; discoidal cell in hindwing not recessed. . . . . *Idomacromiinae*.
4. { Anal-loop slightly longer than wide; median space never traversed by cross-veins. . . . . *Epopthalminae*.  
 Anal-loop slightly wider than long; median space traversed by cross-veins. . . . . *Syntheminae*.

Subfamily *CORDULEPHYINAE* nov. subfam.

This subfamily is erected to hold a single genus *Cordulephya* Selys, which is confined to Australia. The four species belonging to the genus are all frail, graceful insects with rather large wings and long slender abdomen, and are of great interest from their habit of resting with their wings closely apposed over the dorsum as in the *Zygoptera*. The discoidal cells are of archaic shape, with costal side broken and therefore 4-sided cells; the anal-loop is absent and the base of the hindwing, in consequence, as narrow as that of the forewing. In spite of this archaic venation, the antenodal complex is complete, there being but the slightest differentiation between the primaries and secondaries; all triangles are entire; sectors of arculus divaricate from origin or slightly fused; discoidal cell in hindwing incompletely recessed; anal triangle small, entire. Male anal appendages simple, tapering, ventrally spined; female without ovipositor.

The larva is of the *Corduline* type, with large, quadrate head, small, beady, projecting eyes, thorax with a pair of robust spines on dorsum (as in *Oxygastra*), legs long and spidery, abdomen broadly oval. The labium, however, is unique and may be considered as an exaggeration of the most archaic *Synthemine* type, with the serrations deepened to deep clefts on the inner border of the lateral lobe; it seems clear that it is a specia-

lization of this type. The gizzard has 4 folds, two furnished with a single tooth similar to those of the *Cordulegasterinae*, and two with duplicated apices.

This subfamily lies at the root of the *Corduliidae*, from where it has departed on an evolutionary line of its own. I doubt if we have yet solved the problem of these small, zygoterous-like forms of *Libelluloidea*, common to both the families. "Are we really dealing with archaic forms or has the venation undergone a secondary reduction?" The evidence seems to weigh strongly in favour of the latter.

#### Subfamily NEOPHYINAE nov. subfam.

This subfamily is again monogeneric and contains a single form from W. Africa characterized by the discoidal cells with costal side broken, and complete recession of the discoidal cell in the hindwing, as in the subfamily *Corduliinae*. The base of the hindwing is enormously dilated and contains a long, narrow anal-loop. The forewing might well belong to a *Cordulephya*, and the hindwing, apart from its dilatation, to a *Cordulia*. This combination of archaic and recent characters defies solution, and the place of the subfamily remains in doubt. Of the single genus *Neophya* Selys, only a single male specimen is known. Larva unknown.

#### Subfamily GOMPHOMACROMIINAE nov. subfam.

This subfamily contains a number of genera mostly confined to Australia, but two are found in S. America, and a single one in Madagascar, a southern distribution which is not without its significance when taken in conjunction with a similar distribution of the *Petaluridae* and the *Petalinae* of the *Aeshnidae*. They vary considerably in venation but, in all, the discoidal cell of hindwing is incompletely recessed, the triangles are all entire, the sectors of the arculus arise from a common point from which they immediately diverge, the anal-loop is either absent or rudimentary, and, although of some length in some genera (*Nesocordulia* and *Neocordulia*), its midrib zigzags between the cells.

Very few larvae belonging to this subfamily are known, but it may be said that they differ from those of *Cordulephya* by their smaller head, short stout legs, broader abdomen markedly flattened beneath; labium with deep, rather irregular incisions, armed with small spines but few setae.

Genera are: *Hesperocordulia* Till., *Austrocordulia* Till., *Austrophya* Till., *Lathrocordulia* Till., *Pseudocordulia* Till., *Syncordulia* Selys (all Australia), *Gomphomacromia* Brauer, *Neocordulia* Selys (S. America), and *Nesocordulia* MacLach. (Madagascar).

#### Subfamily SYMPETRINAE Tillyard.

This subfamily contains genera which are of the greatest phylogenetic importance since they not only show the evolution of the *Libellulidae* from the *Cordulidae*, but also establish the connection of the *Libelluloidea* with the more archaic *Cordulegasteridae*. The venation in the lowest forms is transitional between the two families of the *Libelluloidea*; the antenodal complex of the genera *Synthemioptis* and *Synthemis* is hardly better developed than in the *Gomphidae*; the primary antenodals are still strong and the secondaries are mostly out of alignment. By examining the older types of *Synthemis*, it is possible to form a series demonstrating the gradual atrophy of the primaries and the gradual alignment of the secondaries. This is preceded by a laying down of accessory basal antenodals, first in

the subcostal space, then in the costal, and finally these two new sets of antenodals come into alignment, at which stage the primaries become obsolescent. Accompanying this process, median cross-veins are found, but what their significance and function is is not quite clear; they apparently become obsolete in the higher forms, as they are altogether absent in the *Libellulidae*. The wings are hyaline and usually uncoloured; the discoidal cells entire, that of the hindwing incompletely recessed; the anal-loop is short and usually wider than long; the sectors of the arculus divergent from origin in the forewing, but slightly fused at origin in the hind; the median space is almost always traversed by one or two veins. The male anal appendages are variable, but usually rather long and sinuous; the female genitalia is transitional, short and atrophied valves in some species, but a long and conspicuous ovipositor in others, very similar to that of the *Cordulegasteridae*.

The larvae in this subfamily are rather variable, but in the lower forms show a remarkable likeness to those of the *Chlorogomphinae*, thus accentuating the affinities of this subfamily to the *Cordulegasteridae*. They are robust, hairy creatures with a frontal plate, cupped labium with deeply serrated borders and numerous setae; the antennae and the structure of the gizzard also conform closely to the larvae of the family mentioned, but the teeth on two of the folds have a bifid apex as in the whole of the superfamily *Libelluloidea*. Tillyard (Proc. Lin. Soc., N.S.W., 35:324, 1910) states: "This remarkable similarity between the larvae of *Synthemis* and *Cordulegaster* is of great phylogenetic importance, for it supplies the missing link between the two great divisions of the *Anisoptera*—the *Aeshnidae* and *Libellulidae*". It is more correct to say "between the *Cordulegasteridae* and *Libellulidae*", and to add that the venation of this genus also demonstrates how the *Libellulidae* have arisen from the *Corduliidae*.

Genera are: *Synthemisopsis* Till. (Tasmania), *Synthemis* Selys (Australia, Papua and New Caledonia), *Eusynthemis* Forst., and *Choristhemis* Till. (Australia).

#### Subfamily IDIONYCHINAE nov. subfam. (Fig. 14.)

Forms in this family are characterized by rather broad wings, large head and small, weak, thorax and slender abdomen. The males are unique in the family by their highly organized and intricate anal appendages; the females by a unique development of the vesicle, which may be conical, bifid or produced into fantastically shaped horns (but in a few species, the vesicle is normal). The wings are hyaline, and, in many females, broadly coloured at the base; discoidal cells entire, that of forewing small and equilateral, that of the hindwing twice as large and a little elongated and incompletely recessed to arculus; sectors of arculus fused for a long distance in fore and hindwings, more so than in any other genera in the family; antenodal complex complete; subtrigone absent; anal-loop a little elongated and with slightly zigzagged midrib; nodus lying far distal to middle of costa and the gap between the bridge and the level of the discoidal cell in the forewing is greater than in any other genus in the family; pterostigma very short; Rspl present, Mspl absent. The female is without an ovipositor and ova are deposited in mud or damp sand alongside streams. The larvae are of the Corduline type described under that family.

This subfamily bears the same relation to the *Corduliidae* as do the *Chlorogomphinae* to the *Cordulegasteridae*, both being tropical offshoots,

the larvae adapted to life in tropical torrential streams. The origin of the *Idionychinae* is doubtful, but I should say that they are an offshoot from the main Synthemine stem. Their distribution extends from the Himalayas and Western Ghats of India to the Sondaic Islands and Borneo.

Genera are: *Idionyx* Selys, and *Idiophya* Fraser.

Subfamily IDOMACROMIINAE nov. subfam.

This subfamily is erected to hold a single aberrant genus whose strangely mingled characters do not permit of its inclusion within any of the other subfamilies belonging to the *Corduliidae*. The wings are broad, the hindwing broadly rounded at the base as in the *Libellulidae*; the reticulation is very close; antenodal complex complete and augmented by accessory basal antenodals and cross-veins in the median space as in genus *Synthemis*; the arculus is recessed to a degree not found in any other genus of the *Corduliidae* and lies at the level of the basal primary antenodal; the discoidal cell is elongate in the width of forewing, and in the length of hindwing, in which it is not recessed to the arculus; anal-loop very long and narrow, and its midrib runs straight between cells; Rspl and Mspl unusually well-developed. Male anal appendages resembling those of the *Epophthalmiinae*. Female unknown. Larva unknown.

There is only a single genus, *Idomacromia* Karsch (W. Africa), and this is known only from a single specimen. Its position in the *Corduliidae* is doubtful; the mixture of archaic and recent characters in its venation presents an insoluble problem. The position of the arculus, the high development of the anal-loop and the rounded base of the hindwing all suggest a recent development.

Subfamily EPOPTHALMIINAE nov. subfam.

In this subfamily we find a very different type of dragonfly, most forms resembling in their robustness and size the Aeshnines rather than the Cordulines. The head is large and globular, the thorax massive, the legs long and spidery; the wings are long and rather pointed at apices; the base in the male strongly angulated and excised. Usually they are hyaline, but in some species there are opaque markings at the base and some patchy amber-tinted suffusion in the body or at the apices of the wings; the reticulation is close; discoidal cells entire or more rarely traversed, that of the hindwing in no way recessed; sectors of arculus fused for a short distance; antenodal complex complete; median space free; anal-loop compact, subquadrate and without midrib; subtrigone in forewing well-defined; anal triangle present; Rspl present, Mspl absent; pterostigma very short. The anal appendages of male are simple, rather short, tapering and acuminate at apex and usually with a short lateral spine. Female without ovipositor; abdomen in the same sex markedly compressed.

Three types of larvae are known, but all agree in having a short, stoutly oval abdomen and usually long, spidery legs. In the genus *Epophthalmia* the head is proportionately small to the body, subquadrate and with the eyes small and projecting upwards like those of a crab; the labium is one of the most formidable organs known in the order *Odonata*; it has a very long movable hook and is deeply fissured along the inner border to form a series of long-pointed teeth which, when meshed with those of the opposite side, remind one of a vermin-trap. In the *Macromias*, the head is larger, the eyes small and projecting more laterally; the abdomen is shorter, more rounded in outline and steeply carinated and

spined dorsally. The labium is typically Libelluline in formation, the movable hook small and the apposed borders of the lateral lobes deeply crenated. The Macromiids are very similar to the last but resemble more closely the larvae of the *Libellulidae*, and their legs are shorter, as in this family. Thus we have a series of larvae ranging from those which closely resemble the more advanced types of *Synthemis*, to the highly specialized ones of *Epophthalmia*. The larval gizzards are remarkably similar in all, to the Libelluline type. From the evidence of the larval characters, it must be assumed that this subfamily split off very early from the Cordulegasterine stem and probably as early as the most archaic types of the *Syntheminae*.

Genera are: *Epophthalmia* Burm. (Oriental and Japan), *Macromia* Rambur (Oriental, Japan and Nearctic: a single species is isolated in Australia and another in far western Europe, these being two of the most extraordinary cases of distribution within the order). *Macromidia* Martin (Oriental and Sondaic Islands), *Didymops* Rambur (N. America), *Phyllomacromia* Selys (Tropical Africa; several species of *Macromia* have been described from Africa, but an examination of their genitalia, which I carried out recently, proves them all to belong to *Phyllomacromia*).

#### Subfamily CORDULIINAE.

This, the largest subfamily of the *Corduliidae*, contains the Cordulines sens. strict., forms which are characterized by the sectors of arc divaricate from their origin, anal-loop nearly as long as in the *Libellulidae* and discoidal cell of hindwing recessed to about the level of the arculus or even slightly proximal to that structure. Generally they are robustly built insects with wings rather broadened at the base, which is either angulated, subrotundate or rounded as fully as in the *Libellulidae*. The reticulation is close; pterostigma moderately long and of Lestine shape; discoidal cells traversed or free, that of hindwing frequently split into 2 or 3 cells; Rspl usually well-defined, Mspl less often so; anal triangle present except in forms with rounded base to hindwing (*Hemicordulia*); arculus situated about midway between the two basal antenodals (but opposite the 2nd antenodal in *Antipodochlora*); antenodal complex complete. Abdomen cylindrical, constricted at segment 3, rather broadened at the end segments; male anal appendages variable, often highly specialized; female without ovipositor.

Larvae with head wider than deep, rounded in front and without frontal plate or horns; eyes small, directed forwards and outwards, thorax with two dorsal spines; abdomen longer than in the other subfamilies, gradually broadening analwards and obtuse at the end, spined dorsally; legs rather long in some, but generally considerably shorter than in other subfamilies.

The subfamily is cosmopolitan in distribution. Genera are: *Anacordulia* Till., *Antipodochlora* Fraser (Australasia), *Hemicordulia* Selys, *Procordulia* Mart. (Papua, Oceania and Australia; one species has also spread to India), *Cordulia* Leach, *Somatochlora* Selys, *Epithea* Burm. (Nearctic and Palaearctic), *Tetragoneuria* Hagen, *Neurocordulia* Selys, *Platycordulia* Will., *Helocordulia* Need., *Epicordulia* Selys, and *Williamsonia* Davis (Nearctic), *Oxygastra* Selys (Palaearctic), *Aeshnosoma* Selys, *Paracordulia* Mart. (Neotropic), *Libellulosoma* Mart. (Madagascar). *Pentathemis* Karsch, is here treated as a synonym of *Aeshnosoma* Selys. Fossil genera: *Miocordulia* Kennedy (Miocene of N. America), *Cordulia* has also been reported from the Eocene and Miocene.

## Family LIBELLULIDAE. (Figs. 3, 13 and 15.)

This enormous complex of forms, varying in size, shape and colouring, is the most dominant of all the *Odonata*. Their success has been due undoubtedly to the taking advantage of adventitious water supplies, and thus we find them, with very few exceptions, breeding in still waters, in strong contrast to the habitats of the *Corduliidae*, which nearly all breed in streams. Unlike this family, few species are coloured metallic, and it is perhaps more than a coincidence that it is these few which breed in running waters. They differ again from the *Corduliidae* by the rounded base of the hindwing in the males, and here, again, it may be more than a coincidence that those forms of the *Corduliidae*, which resemble the *Libellulidae* in this respect, breed in still waters. In other words, the metallic coloured *Libellulidae* and the rounded-winged *Corduliidae* almost certainly represent annectant forms bridging the two families; their morphology and ecology overlap.

Because of this habit of breeding in still waters, and because many such habitats are the creation of mankind, we find a great mass of the *Libellulidae* have forsaken the jungle for open and cultivated country. Moreover, the restricted nature of such habitats leads to overcrowding, a circumstance which leads to mass migration for which many species belonging to this family are notorious.

In addition to the characters noted above, the *Libellulidae* differ from all *Cordulines* by the absence of tibial keels, and also by the great development of the anal-loop, which acquires a more or less stocking-shape. The male anal appendages are very simple and homogeneous throughout the family; the females, except for a few aberrant species in the genera *Sympetrum* and *Uracis*, have no ovipositor.

The task of classifying this large complex has been carried out in a masterly manner by the late Dr. Ris (Cat. Coll. Selys, *Libellulines*, fasc. 9-16) and can hardly be improved upon. The Old and New World, supposedly parallel groups, are here merged into subfamilies because I believe that it is an actual relationship rather than a parallel development which we see; its occurrence throughout the order *Odonata*, and in every family of the order, is so frequent as to cast doubts on such a theory. Roughly, the family may be split up into three groups, a small archaic, corresponding to Group 1 of Ris, a transitional, corresponding to Groups 2, 4 and 5 of Ris, and a recent, which contains the remaining five groups. Group 3 of Ris appears to be an early, highly specialized offshoot from the transitional series. In the ten subfamilies detailed below more than a hundred genera have been described and, since no useful purpose would be served in giving the whole list, I content myself with mentioning those genera which occur in Australia, together with the more dominant ones which belong to each subfamily.

## Subfamily 1. TETRATHEMINAE NOV. subfam. (Fig. 15.)

Species belonging to this subfamily are usually of small size, frequently coloured metallic, marked with red or yellow; the wings are hyaline, rarely coloured, reticulation rather open; discoidal cell of forewing with costal side broken; sectors of arculus fused for a long distance; arculus situated distally between the 2nd and 3rd antenodal veins; Rspl of primitive build, Mspl absent; discoidal field beginning with a single row of cells; anal-loop absent or rudimentary; distal antenodal complete; accessory cross-veins to the bridge and extra cubito-anal veins frequently present. Most forms are found breeding in primaeval jungles in marshy spots beside streams.

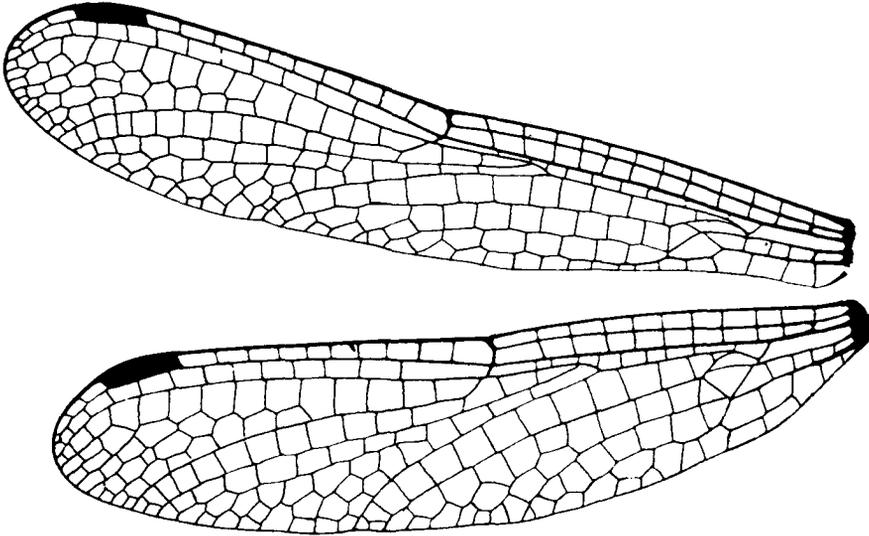


Fig. 15.—Wings of *Tetratheminae* (*Palaeothemis tillyardi* Fraser), male.

Genera are: *Tetrathemis* Selys (Oriental, Ethiopian and Australia), *Nannophlebia* Selys (Papuan and Australia), *Risiophlebia* Cowley, and *Palaeothemis* Fraser (Borneo and Burma respectively) are the smallest species, save *Nannophya*, known in the family, and have the hindwing of no greater breadth than the fore.

#### Subfamily 2. LIBELLULINAE.

Larger species than in the last subfamily and only occasionally coloured metallic; abdomen red, yellow or pruinose bluish; wings hyaline, rarely coloured but occasionally marked at the apices and base; costal side of discoidal cell in forewing shorter than the distal or basal sides and very rarely broken sectors of arculus shortly fused (except in *Libellula*); arculus situated between the 2nd and 3rd antenodals; Rspl well-defined, Mspl absent or vestigial; discoidal field beginning with 2 or more rows of cells; anal-loop variable, usually well-developed; distal antenodal usually complete; accessory cross-veins to the bridge and cubito-anal veins often present. All the forms in this subfamily are still water breeders, although some may breed in sluggish streams.

Genera are: *Lathrecista* Kirby (Oriental, Oceania and Australia), *Amphithemis* Selys, *Lyriothemis* Brauer (Oriental and Papuan), *Orthetrum* Newman (Cosmopolitan, Australia), *Libellula* Lin. (Palaeartic and Nearctic).

#### Subfamily 3. DIASTATOPIDINAE nov. subfam.

This subfamily contains only four genera and is characterized by the relatively broad and dark-coloured wings; venational characters are similar to the last subfamily, but the arculus has moved proximally to between the 1st and 2nd antenodals, and in some of the genera the costal border of

forewing presents a curious sinuous hump near the base of wing. Species in this subfamily, mimic hymenopterous insects in their colour and flight, especially those belonging to genus *Palpopleura*.

Genera are: *Diastatops* Rambur, *Zenithoptera* Selys, and *Perithemis* Hagen (all Neotropical), *Palpopleura* Rambur (Oriental and Ethiopian).

#### Subfamily 4. BRACHYDIPLACINAE NOV. subfam.

Two so-called parallel groups, belonging to the Old and New World respectively, make up this subfamily, which is characterized by a number of archaic or transitional formations in the venation; sectors of arculus fused at origin; the veins Riii, IRiii and Rspl all of primitive build; usually accessory cross-veins to the bridge and extra cubito-anal veins; discoidal cell of hindwing situated distal to the line of arculus; anal-loop variable but well-defined; arculus lying between the 1st and 2nd antenodals.

Genera are: *Nannophya* Rambur (Oriental and Australia), the smallest species in the family *Libellulidae*; *Uracis* Rambur (Neotropical), characterized by a secondary development of the ovipositor which resembles that of *Cordulegaster*; *Fylgia* Kirby (Neotropical), has the discoidal cell of forewing with costal side broken as in *Tetrathemis*, but its other venational characters are well advanced; *Oligoclada* Karsch, and *Microthyria* Kirby (Neotropical), both dominant genera.

#### Subfamily 5. SYMPETRINAE NOV. subfam.

This subfamily contains species of moderate size and non-metallic colour. The wings are hyaline, coloured or not, reticulation close to very close (excessively so in genus *Neurothemis*, where the basic venation is reinforced by a dense network of smaller veins); arculus between the 1st and 2nd antenodals; sectors of arculus fused for a short distance at origin; Rspl and Mspl well-developed; anal-loop lengthened and stocking-shaped; anal field filled with rows of cells in the width of wing; archaic features such as accessories to the bridge, etc., absent.

Genera are: *Nannodiplax* Brauer, *Neurothemis* Brauer, and *Diplacodes* Kirby (all Oriental, Papuan and Australia, the latter genus also Ethiopian), *Crocothemis* Brauer (Oriental, Ethiopian and Australia), *Brachythemis* Brauer (Oriental and Ethiopian), *Sympetrum* Newman (Cosmopolitan, but not Australian), *Erythemis* Hagen, and *Erythrodiplax* Brauer (dominant in the Neotropics).

#### Subfamily 6. LEUCORRHININAE NOV. subfam.

A small subfamily containing only four genera with venational details similar to the last but differing by the discoidal cell of forewing with a much longer costal side and the sectors of the arculus separated at origin as in the *Corduliinae*. Archaic characters such as accessory cross-veins to the bridge and extra cubito-anal veins are frequently present; the arculus is however recessed to between the 1st and 2nd antenodals. Species belonging to the group have the wings more or less brightly marked and coloured.

Genera are: *Leucorrhinia* Britt. (Palaeartic and Nearctic), *Celithemis* Hagen, *Planiplax* Muttkow., and *Brachymesia* Kirby (Nearctic and Neotropic; the former closely parallels the genus *Rhyothemis* in the colour and markings of its wings).

#### Subfamily 7. TRITHEMINAE NOV. subfam.

I include in this subfamily all those genera belonging to group 8 of Ris, but excluding *Onychothemis* and *Zygonyx*. Species are characterized

by a movement of the nodus distalwards or the apical portion of the wing is shortened; the anal-loop is highly developed and its outer angle extends well beyond the level of the discoidal cell; the anal vein bordering it outwardly is bent to a right angle; the venation is essentially recent and all archaic features have disappeared. Both size and colour vary widely and species may be entirely black or brightest red; the females are generally some colour approaching dull ochreous.

Genera are: *Austrothemis* Ris (the only representative in Australia), *Trithemis* Brauer (Oriental and Ethiopian), *Pseudothemis* Kirby (very large, robust species from Japan), etc.

#### Subfamily 8. ONYCHOTHEMINAE nov. subfam.

I include here two genera whose general facies and habits stand wide apart from the rest of the others in subfamily *Tritheminae*. Of these, *Zygonyx* Selys, so closely resembles the *Corduliidae* that it was at one time classed with them; the species, which are numerous and mainly Ethiopian, are generally steely-black, marked strikingly with yellow; the abdomen is long and narrow and bears an identification mark on segment 7, as in many *Macromias*. It is a riverine breeder and is usually to be seen patrolling or hovering in mid-stream. The other genus, *Onychothemis* Brauer, is also a riverine breeder and hawks swiftly up and down over a measured beat of its stream; it is of robust Libelluline shape, but is coloured green or coppery metallic marked with yellow as in many *Corduliidae*. The venation, in both, is similar to that of the *Tritheminae*, but the base of discoidal cell of hind-wing is usually slightly proximal to the level of the arculus.

#### Subfamily 9. RHYOTHEMINAE nov. subfam. (Fig. 13.)

This is a monogeneric subfamily erected to hold a number of highly specialized forms characterized by their mimicry of *Rhopalocera* and *Hymenoptera*. Their wings are broad, rather short in some, and variable in shape in the sexes of others; heteromorphic females occur frequently in the latter group. The body, which is dark metallic, is never fully chitinized, apparently to reduce its weight. Thus the flight is fluttering or soaring, dependent more on the air currents than the insect's volition, and this together with the bright black and gold colouring of the wings, renders them remarkably like butterflies when in flight. Others have the bases of the wings dark metallic blue-black and, as this part only is visible during flight, they resemble very closely certain aculeates with which they associate. The venation is similar to that of the next subfamily with which Dr. Ris classed them, but the veins Riv + v and MA curve gently and evenly down to meet the border of the wing, instead of being strongly angulated towards the distal ends. The abdomen is very short and little more than half the length of the wings.

Genus: *Rhyothemis* Hagen (Oriental, Ethiopian and Australia).

#### Subfamily 10. ZYKOMMATINAE nov. subfam.

This subfamily corresponds to the 10th or *Tramea* group of Ris and contains species usually of large size, with large head, small thorax and very long, pointed wings, broadened at the base of the hind. The nodus is situated far out; pterostigma very small and inconspicuous; sectors of arculus fused shortly or separated from origin; anal-loop very long, apical portion as long as or longer than basal and with outer angle rounded or acute; discoidal cell of forewing remarkably narrow in width of wing, its

apex directed strongly basalwards; Rspl and Mspl highly developed and concave to IRiii and MA respectively. The abdomen is narrow, cylindrical and somewhat constricted at segments 4 and 5; the male anal appendages are long and narrow. In the *Trameas*, venation may be said to reach perfection.

Genera are: *Zygomma* Rambur (Oriental, Ethiopian and Australia), *Tholymis* Hagen (Circumtropical); these two latter genera are remarkable for having the apex of the anal-loop open. *Pantala* Hagen, and *Tramea* Hagen (Circumtropical and Australia), *Camacinia* Kirby, *Hydrobasileus* Kirby, *Macrodiplax* Brauer, and *Aethriamanta* Kirby (all Oriental, Papuan and Australian), *Urothemis* Brauer (Ethiopian, Oriental and Papuan).

In the preparation of this paper many hundreds of references have been made, and it is obviously impossible with the space at my command to give even a tenth of these. A number of relative ones have been given in the text and a few of the more important ones are listed here:—

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#### ADDENDA ET CORRIGENDA TO PART II.

- p. 199. The text-figures here and on p. 214 have been transposed.  
 p. 200. After "*D. apicalis* (Fraser)" on line 5 from bottom of page, read straight on to next para.  
 Line 3 from top of page, read "Agriodea" for "Agriodea".  
 p. 202. In couplet 3 of Key, for ";" after "basal", substitute a hyphen.  
 p. 209. For "*Protophore*" on line 25, read "*Protothore*".  
 p. 210. Add to list of genera at bottom of page the following:—"Fossil genera: *Zacallites* Cock. (Eocene), *Epallagites* Cock. (Eocene), *Euphaeopsis* Handl. (Jurassic), *Pseudoeuphaea* Handl. (Jurassic)."  
 p. 214. The text-figures here and on p. 199 have been transposed. On line 4 of legend, read for "*Ditaxineura*", "*Diphlebia*". On lines 14 and 8 from bottom of page, for "10" read "9".
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