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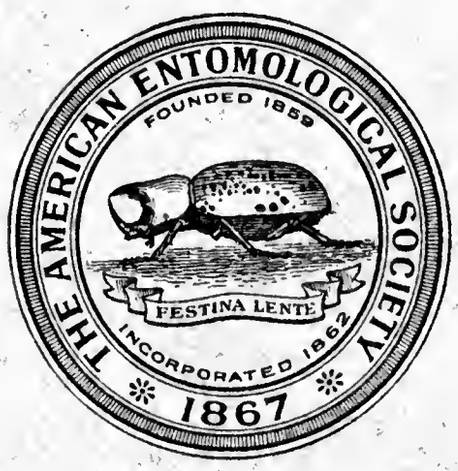
AMERICAN ENTOMOLOGICAL SOCIETY
NUMBER 3

A VENATIONAL STUDY OF THE SUBORDER ZYGOPTERA

(ODONATA)

WITH KEYS FOR THE IDENTIFICATION OF GENERA

BY
PHILIP A. MUNZ



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AT THE ACADEMY OF NATURAL SCIENCES
PHILADELPHIA
1919

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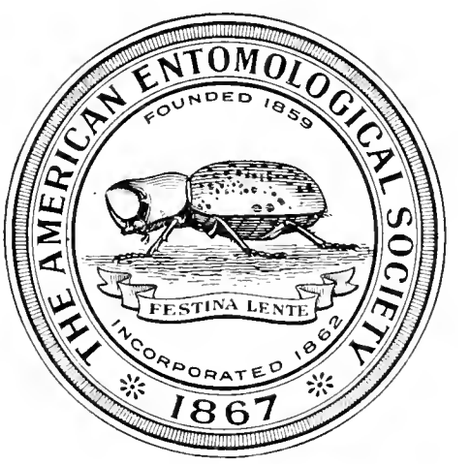

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I—INTRODUCTION

At the present time it is not necessary to offer either explanation or excuse for the use of venation as a guide to the phylogeny of a group of insects, particularly of any of the Neuropteroids, the exceedingly rich and varied veining of which has been the basis of many excellent pieces of work. The purpose of this paper is to make the fullest possible use of wing-veins as a means of interpreting relationships and as a method of identifying the genera of one of the suborders of the Odonata, the Zygoptera. It must be remembered, however, that venation is not the only index to genealogy, nor perhaps always the most reliable, but it is one of the most evident and fundamental and therefore most valuable methods which we have to enable us to determine relationships. In some cases, without doubt, a study of genitalia and morphology will throw more light on the situation and even change some of our conceptions which have been arrived at from the study of the wings only.

The nomenclature of the veins of the Zygoptera and their homologies to those of other groups have been thoroughly worked out, but, since the days of Baron de Selys, no attempt has been made to consider the whole suborder in detail and to make keys for identification. A word of explanation may be permissible in regard to the keys herewith submitted; I have examined such material as I have had access to in an endeavor to make them as generally applicable as possible; but in some cases descriptions only could be used, since during the past two years correspondence with many European workers and hence the securing of many desirable figures have been impossible. I feel, however, that the paper is justifiable, if for no other reason than to have in one place in the literature such wing-photographs as have been collected in the course of the work, the venation of many genera not having been published before.

Acknowledgements

To the many who have kindly contributed material and suggestions for this study my gratitude is due and is thankfully given. This problem was undertaken at the suggestion and under the direction of Professor James G. Needham, whose unfailing interest

and valuable criticism have made possible what has been accomplished. He has been very generous in the time and abundant material which he has given me. Mr. C. H. Kennedy, also of Cornell University, who has been working on the same phylogenetic problem from another method of approach, has never hestitated in giving me suggestions arrived at from his study, has made several drawings for me and brought material from museums which I was not able to visit. Dr. P. P. Calvert and Dr. Henry Skinner of Philadelphia very generously loaned specimens and permitted the use of the extensive collections at the Academy of Natural Sciences of Philadelphia. Mr. Carl Ilg of Philadelphia kindly copied several descriptions which were not available at Cornell. Mr. E. B. Williamson of Bluffton, Indiana, loaned valuable material; Dr. Samuel Henshaw of Cambridge sent material for study and permitted Mr. E. Avery Richmond of Cornell to photograph several specimens at the Museum of Comparative Zoology. Mr. Rolla P. Currie and Miss Currie were very kind and helpful in allowing me the use of the collections at the National Museum. Dr. W. J. Holland and Mr. Hugo Kahl of the Carnegie Museum permitted Mr. Kennedy to bring several specimens to Ithaca and to study others at Pittsburg. Mr. Herbert Campion and Mr. F. W. Campion sent several photographs of specimens at the British Museum. Dr. F. Ris of Rheinau, Switzerland, kindly sent proof-sheets of an article expressing his views on the venation of the Zygoptera, and Mr. R. J. Tillyard of New South Wales, Australia, sent several papers dealing with the same subject and with new and rare Australian Zygoptera. To all of these contributors is due much of the success in the completeness which it has been possible to secure.

Nomenclature of the Wing-Veins

The Comstock-Needham system of naming the veins has come into very general use among workers on the Odonata since the Genealogic Study by Professor Needham in 1903; and it is to be retained in all its essentials as presented in his paper. Tillyard, however, (1914) showed that the vein formerly known as A is in reality partly a secondary structure built back toward the base of the wing from one of the so-called "cubito-anal" cross-veins and

that the vein A at the base of the wing is fused with Cu, but crosses the space back of Cu and then proceeds as formerly thought toward MA. He therefore proposes the name "anal-crossing" (Ac) for this apparent cross-vein, and the abbreviations Ab for the bridge toward the wing-base, and A′ for the distal portion of the anal vein. This system will be used in this paper when especial attention is called to some part of this vein, otherwise A alone will be used to designate the anal vein in general; the sign 1st A is not necessary since the Zygoptera possess only one anal vein. I agree with Mr. Tillyard that the sign A followed by an asterisk as used by Dr. Ris is unfortunate; when I read one of his descriptions I find myself involuntarily looking to the bottom of the page for the foot-note which I always associate with the use of the asterisk.

Mr. Tillyard's contention (1915) and that of Dr. Ris (1916a) that the Zygoptera present a different condition than that of the Anisoptera in the branching of the radius do not seem well founded. To be sure none of the nymphs of the Zygoptera that have yet been examined show the trachea R_s crossing over that of M_{1+2} as do the Anisoptera, however it seems inconceivable that the vein R_s of the Anisoptera can have in the Zygoptera a vein so completely analogous in position and yet not be homologous. Mr. Tillyard's name "median sector" is a matter of words only; it indicates no homology to the veins of any other order, although in retaining the same name for the different branches of media he admits that the media has exactly the same position in both suborders, which state cannot be true if the radius does not present the same condition in both. Professor Needham (1917) has shown how many of Mr. Tillyard's arguments can be used to support the opposite view of the case. I therefore have no hesitation in following the usual system of nomenclature.

As an example of the Agrionidae the genus *Agrion* (*Calopteryx*) may be used with the abbreviations given in fig. A. These abbreviations are given as follows:

C = costa, Sc = subcosta; R_1 = radius-one, R_s = radical sector; M_1 = media-one, M_2 = media-two, M_3 = media-three, M_4 = media-four, M_{1a} = the longest sector between M_1 and M_2; Cu = cubitus, Cu_1 = cubitus-one, Cu_2 = cubitus-two, Cu_{2a} = a branch of Cu_2

arising just beyond MA; A = first anal vein, Ac = anal crossing, Ab = anal bridge, A′ = anal vein from Ac to MA; N = nodus, Sn = subnodus; St = stigma, B.S. = basal space, B.R.S. = basal radial space; An = antenodal cross-veins, Pn = postnodal cross-veins, Ar = arculus, MA = medio-anal link; Q = quadrangle, Sq = subquadrangle.

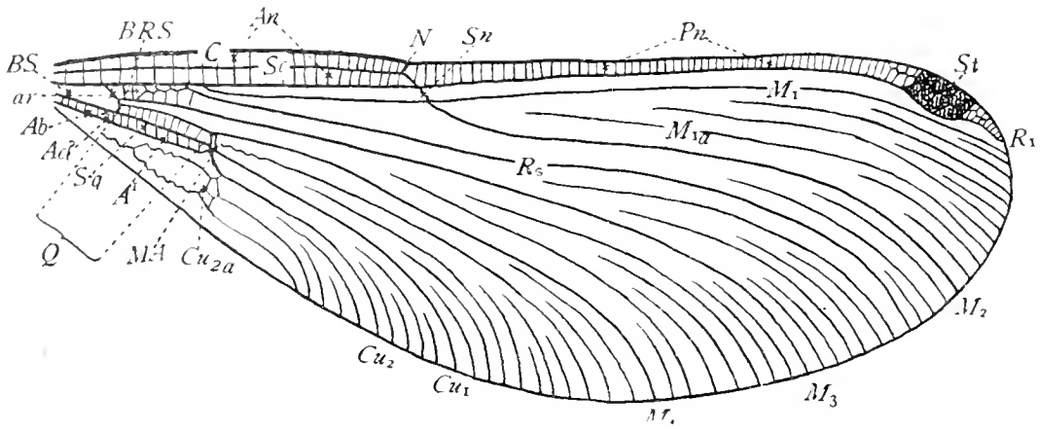

Fig. A. Venation of *Agrion* (*Calopteryx*).

These terms are all familiar ones and need for the most part no definition here. The *subquadrangle* is that space between Ac and MA, and between Cu and A, or Cu and the hind margin of the wing when A′ is not present. Ac cannot always be located because of the numerous cross-veins between Cu and A to be found in some genera, but can generally be distinguished by its obliquity. The term *medio-anal link* is one defined by Mr. Williamson (1913) "as the cross vein forming the distal end of the quadrangle and that part of Cu_2 opposed to Cu, and placed transversely to the long axis of the wing." *Supplementary sectors* are those longitudinal veins present between the principal veins. The quadrangle, subquadrangle, basal space, and basal radial space are said to be *crossed* when they have cross veins, and are *free* when without cross-veins. The basal radial space is *open* when M_{1+2} does not touch R, and *closed* when M_{1+2} fuses with R. Of the antenodals there are two series: those of the *first* or *costal* series, i.e. those between C and Sc; and those of the *second* or *subcostal* series, i.e. between Sc and R.

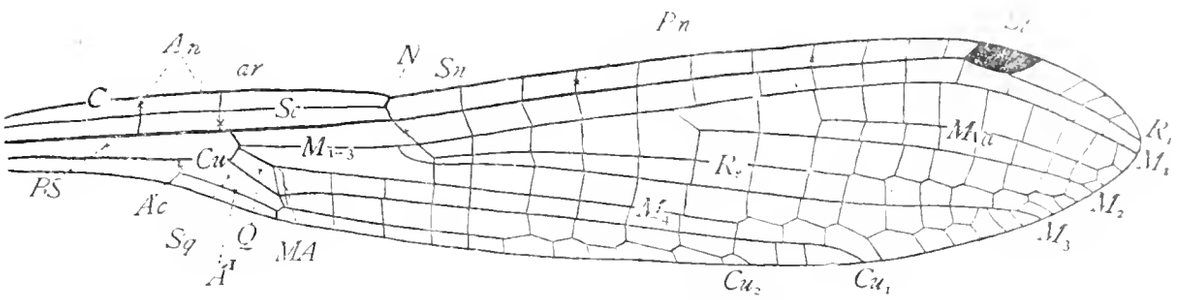

Fig. B. Venation of *Argiocnemis*.

As an example of a wing of the *Coenagrionidae*, *Argiocnemis* may be used, for which see fig. B. The notations are largely as in fig. A, except that there is no *basal radial space* present and that the antenodel spaces are few enough to be numbered; the *first antenodal space* is that between the base of the wing and the first antenodals, the *second antenodal space* is that between the first and second antenodals, and the *third antenodal space* is that between the second antenodals and the nodus. Cu_{2a} is not present.

Explanation of Figures

In referring to figures, A, B, C, etc. are the text figures, while figures 1, 2, 3, etc. are to be found in the plates at the end of the paper.

II—A DISCUSSION OF THE PHYLOGENY

Passing now from a review of the system of nomenclature used, the next step is the consideration of the phylogeny of the Zygoptera and their relationship to other groups.

The Anisozygoptera

In his treatise on fossil insects, Handlirsch (1906–1908) created as a new suborder the Anisozygoptera, for many fossil forms and for the living genus *Palaeophlebia*, to which he gave the name *Neopalaeophlebia*, since the former name was preoccupied. Dr. Calvert (1903), however, had already used the name *Epiophlebia* for *Palaeophlebia* and it is his name that must be used. This genus according to Handlirsch falls as readily into the Anisoptera as the Zygoptera and to keep the two groups distinct, a third intermediate one is necessary. *Epiophlebia* (fig. 1) is the only known survivor of a large suborder of Mesozoic insects and is

therefore of considerable importance phylogenetically. Hence, while it is not now one of the Zygoptera, it deserves discussion in this paper.

Aside from its venational primitiveness it has been shown by Schmidt (1915) to be intermediate between the two modern suborders in the structure of the male genitalia of the second and third abdominal segments. Mr. Kennedy informs me that this is so obviously the case that only a separate suborder will suffice to show its points of difference. The broad area between M_4 and Cu_1 just beyond MA; the shape of the quadrangle, especially that of the hind wing where a cross-vein in the right position would give the supertriangle and triangle of the Anisoptera the zigzag condition of the supplementary sectors,—all these are venational features which justify its position as something quite distinct from the Zygoptera. In itself it does not need to be taken as a form from which the Zygoptera and Anisoptera have descended, in fact it cannot be so considered, but it does show affinities with both and, as a survival of the ancestral group from which our two modern suborders have sprung, it is worthy of note.

The Zygoptera Proper

The Zygoptera may therefore evidently be considered as derivatives of the Anisozygoptera. They may themselves be divided into two families, which were long made subfamilies by workers on Odonata. It would be very desirable and lead to much less confusion if these families could retain the old names; Calopterygidae and Agrionidae, but since most writers on the group have recently followed Kirby's Catalogue in using the genus names *Agrion* and *Coenagrion* rather than *Calopteryx* and *Agrion*, and since Muttkowski (1910) has brought additional evidence to show that these are the names to be used, I shall follow their example and speak of the old group Calopteryginae as Agrionidae and of the former Agrioninae as Coenagrionidae.

Of the generic names proposed, about one hundred and eighty now seem valid and are recognized in the keys hereto appended. Of these about forty come in the first family, the Agrionidae, which is the more generalized of the families and ends in forms very closely related to some of the Coenagrionidae. The two

families, in fact, do not form a dichotomy, but the one leads to the other and is connected with it by so many genera that the dividing line is in some cases difficult to find. In a general way the former one is characterized by the presence of several to many antenodals and by cross-veins generally being present in the quadrangle and subquadrangle. M_3 separates from M_{1+2} nearer to the arculus than to the subnodus, and the nodus is far out in the wing, at from one-third to one-half of the length of the wing. These tendencies in venation are all fairly constant and, as will be shown later, indicate a rather primitive condition. The Coenagrionidae, on the other hand, have two antenodals generally and no cross veins in the quadrangle or subquadrangle, with but few exceptions. In one line only, that of the Lestinae and Lestoidinae, does M_3 retain its original condition of branching off from M_{1+2} near the arculus, in the other groups its point of origin migrates outward. The nodus, however, is drawn toward the base of the wing and ranges in position from about one-seventh to one-third of the length of the wing. The more detailed account of the exact steps in phylogeny may better be discussed under the families and subfamilies.

The *Agrionidae*

As was said before, this family includes the old group Calopteryginae which was divided by de Selys into five legions: *Thore*, *Calopteryx*, *Euphaea*, *Libellago*, and *Amphipteryx*. Venationally these five groups are better arranged in three subfamilies, as was done by Professor Needham (1903a), which I shall call: Polythorinae, to include the legion *Thore;* Agrioninae, for the legion *Calopteryx*, and the Epallaginae, for the last three legions. To these must now be added a fourth subfamily, the Disparocyphinae for the genus *Disparocypha* (fig. 37), recently described by Dr. Ris (1916b). This very remarkable genus will be discussed later with the reasons for its segregation from the others.

The affinities of the Agrionidae with *Epiophlebia* (fig. 1) are evident enough: the large number of antenodals, the origin of M_3 far before the subnodus, and the location of the nodus far out in the wing.

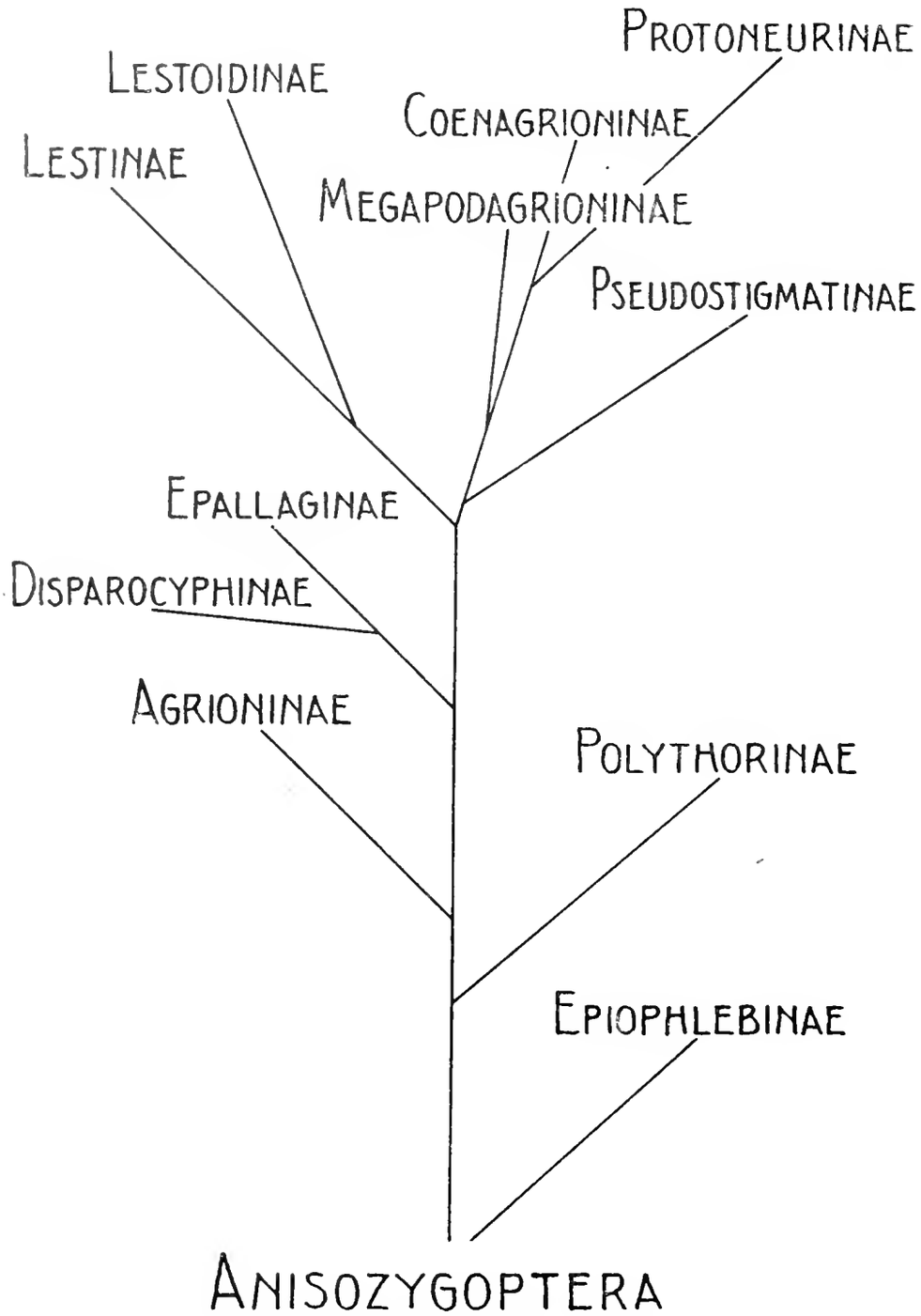

Fig. C. Proposed Phylogenetic Tree for the Zygoptera.

The Polythorinae

The most sharply differentiated group of the Agrionidae, in that it differs most from the others, is the Polythorinae. In it M does not descend the arculus to any extent, so that the quadrangle is very much wider proximally than distally and is concave anteriorly.

This peculiar little group of four genera is a rather compact one, but shows within itself the ever present tendencies of specialization to be found in the other subfamilies. It retains a rich venation with many cross-veins, but has these fewer in number in the higher genera, has petiolation become more advanced, has some of the sectors tend to become attached to the principal veins, and has M_2 becoming branched from M_1 beyond the subnodus. *Polythore* (fig. 2) and *Euthore* (fig. 3) are the two more generalized, *Cora* (fig. 5) and *Chalcopteryx* (fig. 4) the two more specialized genera. The fact that the Polythorinae are discussed first does not mean that they are the most generalized Zygoptera; their quadrangle and the continuing of the direction of M_{1-3} by M_{1+2} rather than by M_3, as well as their petiolation, gainsay this. However, they are the most distinct group and must have separated from the others at rather a low level.

The Agrioninae

Venationally this group is quite distinct from the Epallaginae; however, Schmidt (1915) working on the male genitalia, finds there no basis for such a division. The Agrioninae consists of the Vestalinae as defined by Dr. Needham (1903a) and can be distinguished from the Epallaginae and Disparocyphinae by the following venational tendencies: M_{1a} has a course parallel to that of M_2, the stigma becomes diffuse and finally atrophies altogether; and the vein Cu_2 in most forms has a branch Cu_{2a} running toward the hind margin of the wing. *Vestalis* (fig. 18), *Heterina* (fig. 19) and *Lais* (fig. 20) do not possess this branch, but the facts that the stigma may be lost, that M_{1a} is parallel to M_2, that the quadrangle becomes convex above, that some of the sectors tend to become attached to the longitudinal veins, and that there is no petiolation, and but slight reduction in the number of antenodals, indicate affinities with the Agrioninae rather than the Epallaginae. The subfamily Agrioninae has its own methods of specialization, but its line ends in itself and shows no relationship to higher forms.

Aside from the *Vestalis-Heterina-Lais* group, which is the most distinct, the remaining genera can be divided into those which have Cu_{2a} running perpendicular to the hind margin of the wing or toward the base of the wing, and those in which it is bent away

from the base of the wing. The former group begins with such genera as *Archineura* (fig. 8) and *Echo* (fig. 7) and continuing through *Umma* (fig. 9), *Sapho* (fig. 10) and *Agrion* (fig. 11), ends with *Matrona* (fig. 13), *Matronoides* (fig. 12), and *Neurobasis* (fig. 14). The latter group consists of *Mnais* (fig. 15), *Psolodesmus* (fig. 16), and *Phaon* (fig. 17), which approach *Vestalis* (fig. 18) in some respects; for example in the attachment of sectors, in the convexity of the quadrangle above, and in the general wing proportion and number of cross-veins.

The Epallaginae

The discussion now leads to perhaps some of the most generalized of living Zygoptera: the genera *Pseudophaea* (fig. 21) and *Dysphaea* (fig. 22). It is here that one must look for the beginning of the line which leads to the higher family by reduction in the number of cross-veins and of the supplementary sectors, by the location of M_{1a} halfway between M_1 and M_2, and especially by the bending of M_3 and R_s away from M_{1+2} so that it is the latter vein rather than M_3 which continues the direction of M_{1+2+3}. All the genera so far discussed under the Zygoptera, except the Polythorinae, have M_3 in line with M_{1+2+3}, but in the higher members of the Epallaginae it is no longer the case. Petiolation too proceeds to a high degree of advancement and the stigma persists. Beginning then, with *Pseudophaea* (fig. 21) and *Dysphaea* (fig. 22) a series can be arranged (as has been done in the key to the Epallaginae) which proceeds by reduction and petiolation through *Bayadera* (fig. 23), *Epallage* (fig. 24), *Anisopleura* (fig. 25) and *Rhinocypha* (fig. 26) to *Micromerus* (fig. 28) where the new condition is first evident as regards the base of M_3. *Rhinocypha* (fig. 26), *Libellago* (fig. 27), and *Micromerus* (fig. 28) form rather a compact and distinct group with M_4 arching forward and Cu_2 backward, more so than in the related genera and with R_s and M_2 parallel at their tips and with two prominent sectors between. *Cyanocharis* (fig. 29), *Caliphaea*, *Heliocharis* (fig. 30), *Dicterias* (fig. 32) and *Neocharis* (fig. 31) carry on the reduction process until in *Devadatta* (fig. 33) and *Amphipteryx* (fig. 34) the continuing of M_{1+2+3} by M_{1+2} is again evident and firmly established. *Diphlebia* (fig. 34) is enough

like a low form of the Lestinae to be taken for one but for the presence of too many antenodals; and in *Philogaiga* (fig. 36) is to be seen the beginning of the tendency for R_s and M_3 to arise nearer the subnodus. Thus the evolutionary steps in the Epallaginae are in marked contrast to those in the Agrioninae.

The Disparocyphinae

The genus *Disparocypha* (fig. 37) is placed by Ris in the legion Libellago and it is clearly related to that group. But its characters of difference are so great that to be consistent with the arrangement in the higher subfamilies, it must be placed in a separate one. It differs from the members of the legion Libellago as much as the Protoneura group does from the Coenagrion group or the genus *Lestoidea* (fig. 45) from *Lestes*. Cu_1 is short, not extending to the level of the subnodus; Cu_2 is reduced to a cross-vein; A ends in the hind margin of the quadrangle; M_4 is almost perfectly straight in its entire length; and the stigma is very much broader distally than proximally.

This reduction of Cu_1 and Cu_2, which seems to be a very highly specialized tendency, will be discussed again under *Lestoidea* (fig. 45) and *Protoneura*. Its occurrence in three widely separated groups is indeed an interesting parallelism.

The *Coenagrionidae*

As the two families now stand they can conveniently be separated by placing in the Agrionidae those genera with five or more antenodals and with M_3 arising nearer the arculus than the subnodus. Of the Coenagrionidae those with more than two antenodals have M_3 arising near the subnodus and often have the nodus very near the base of the wing, while those with M_3 arising near the arculus have only two antenodals. Now from this state of affairs it is evident that the division into two families is somewhat artificial and yet, I think, it is a tenable one and it certainly is convenient. The higher family includes only more specialized forms than the lower; the only difficulty in the whole situation is that our series from one to the other is too complete to make the divisions clearly marked. From the phylogenetic standpoint this condition is of course fortunate. *Diphlebia* (fig. 34) and related genera show very evident affinities to the Lestinae among the

Coenagrionidae, especially in the position of the base of M_3 and of R_s and in the petiolation and general arrangement of veins. It connects the Lestinae to the Epallaginae through the genera *Pseudolestes* and *Ortholestes*, and differs from these forms chiefly in the number of antenodals. On the other hand, the Lestinae are related very closely to the Megapodagrioninae by *Rhipidolestes* (fig. 52). Yet in this same group of Megapodagrioninae it is necessary to include *Thaumatoneura* (fig. 51), which with its number of antenodals and abundant sectors indicates a descent from some Agrionid, possibly one like *Philoganga* (fig. 36) in which the quadrangle is short, and M_3 and R_s arise at some little distance beyond the arculus. The retraction of the nodus in a form like *Philoganga* would bring about a condition comparable to that in *Thaumatoneura*, except for the numerous sectors and many crossveins of the latter. As will be shown later, *Thaumatoneura* in turn leads to the Pseudostigmatinae and to the other Megapodagrioninae, which by reduction approach the Coenagrioninae and these in their turn are connected with the Protoneurinae. After this additional evidence is presented, it will be seen that it is a very logical thing to consider the Coenagrionidae merely a specialized offshoot or number of offshoots from the Agrionidae, as arranged in the tree in Figure C.

In this connection the following quotation is of interest. Tillyard (1914b) in discussing the classification of the Zygoptera declares, "It becomes now more than ever apparent that the Selysian division into *Calopterygidae* and *Agrionidae* is quite untenable as a natural dichotomy, more than this, it is pretty clear also that the *Zygoptera* are not like the *Anisoptera*, derived from an original pure line descent. Triangle-formation most certainly started once; and, however far back new fossil discoveries may take us as regards the first formation of the triangle, there can be no doubt about the origin of all *Anisoptera* from that single line of descent, which Palaeontology already places as far back as the Trias, and which probably began in the Permian period. Most of the *Zygoptera* (certainly all those with regular quadrilaterals) must have branched away from the *Anisoptera*-line before this. But who can tell how

many separate branchings took place, even amongst this one portion of the Suborder? The origin of the tribe *Agrionini*[2] is doubtful, for their acute quadrilateral might yet be proved to be the reduced remnant of an originally weak *Anisopterid* triangle-formation. Finally, standing out clear from all the rest as the most recent offshoot from the *Anisopterid* line, we see the *Epiophlebia-Synlestes-Lestes* line of descent, which branched off from that line *not very far from* the beginnings of the *Gomphinae*, and whose sharply angulated quadrilateral is almost certainly an *Anisopterid* remnant."

Following out his theory, Mr. Tillyard places this "line of descent" in a family Lestidae and divides it into the following subfamilies: Epiophlebinae, Lestinae, Synlestinae, and Heterophlebinae, the last named containing fossils only. It is now known that *Epiophlebia* (fig. 1) is far from being near the Lestinae not only venationally, but on the basis of the genitalia, it is of far too generalized a nature to be placed near them, although an oblique vein between M_2 and R_s is present in both subfamilies and many of the sectors are very zigzag. The Zygoptera cannot be considered as derived from the Anisoptera, but form a dichotomy with them, both arising from the ancient Anisozygoptera. The argument that all Zygoptera with the regular quadrangle are primitive is also unfounded; the regularity of the quadrangle, that is, its squareness distally, is not so fundamental a thing as it might seem. Those forms which are perhaps the most highly specialized, those in which Cu_2 is reduced to a cross-vein, have the square quadrangle; yet this condition arises independently three times, in *Disparocypha* (fig. 37), in *Lestoidea* (fig. 45) and in the Protoneurinae. I cannot, therefore, agree with any of the views expressed in the above quotation as regards the phylogeny of the Zygoptera. This subject can, however, be more fully discussed in treating each subfamily independently.

The Lestinae

The Lestinae, as has been said before, include those Coenagrionidae in which the vein M_3 arises nearer the arculus than the subnodus, therefore it comprises the legion *Lestes* of de Selys. This feature is an ancient and primitive one and specialization in this

[2] Agrionini is Coenagrionidae of this paper.

group has been in a different direction from that in the other Coenagrionidae. The presence of the *oblique* vein between M_2 and R_s is of course a character recalling the condition to be found in the *Anisoptera*, but it seems to be a rather dangerous one on which to depend too extensively if it means that *Epiophlebia* must be placed in the same category as the Lestinae. *Pseudolestes* (fig. 38) and *Ortholestes* (fig. 39) have the general venation of the Lestinae and are intermediate between the higher Lestine genera and *Diphlebia* (fig. 34). Yet they do not possess the oblique vein, at least it is not distinct. Cannot this cropping out of a primitive feature be a secondary matter, a reappearance? It is evidently so in the case of the square quadrangle of *Protoneura*, *Lestoidea*, and *Disparocypha*. A single character is dangerous to use too far to the exclusion of others, although it may sometimes seem necessary to do so. The oblique vein is present also in *Chlorolestes* (fig. 66) and *Synlestes* (fig. 63) yet the rest of the venation does not suggest the Lestinae. This oblique vein is of course present in those genera in the nymphs of which the trachea for R_s is joined to the trachea for M_2. Whether this attachment of the trachea is to be taken as more or less important than the adult venation is the question. It seems reasonable to lay more stress on the latter since in it several other characters unite in placing *Chlorolestes* and *Synlestes* in the Megapodagrioninae.

Pseudolestes (fig. 38), *Ortholestes* (fig. 39) and *Rhipidolestes* (fig. 52) show a connection between the Lestinae and Megapodagrioninae, and these two subfamilies can be considered as offshoots from the same general region of the Agrionidae. Their close affinity warrants the retention of the subfamily name for the Lestinae rather than the use of a family name. Of the forms included here under Lestinae *Pseudolestes* (fig. 38) is undoubtedly the most primitive, in having the quadrangle like that of *Diphlebia* (fig. 34) and in its large number of supplementary sectors. *Ortholestes* (fig. 39) comes next and is followed by the Lestine genera proper: *Archilestes* (fig. 40), *Megalestes* (fig. 41), *Orolestes*, *Platylestes*, *Lestes* (fig. 44), *Sympycna* (fig. 42), etc. The general tendency is that of reduction, combined with straightening of the veins at the tips. Many sectors and veins are somewhat zigzag, and there develops

also a narrowing and sharpening of the quadrangle distally. Petiolation does not proceed very far, never to the level of the arculus.

The Lestoidinae

Mr. Tillyard (1912a) described as a new genus a very peculiar form which he called *Lestoidea* (fig. 45) and for which he proposed a new legion of the same name. This remarkable insect has decided Lestine affinities in the location of the base of M_3 and R_s, but has the vein Cu_2 reduced to a cross-vein and Cu_1 but one cell long. Yet in addition to the above characters it is distinguished from all Protoneurinae by the presence of two sectors between M_1 and M_{1a}.

The decrease in length of Cu_1 and Cu_2 is one of the most extreme tendencies in specialization occurring in the Zygoptera and its origin in the various groups is an interesting parallelism. As always happens when Cu_2 is thus reduced MA is straightened and the quadrangle ends squarely. The retention of the two sectors between M_1 and M_{1a} is rather remarkable, in view of the fact that all others are gone and that in none of the Lestinae are there any long sectors between these two veins. *Lestoidea* must therefore have arisen from some rather ancient form and is distinct enough to merit a legion for itself or in the system here used, a subfamily.

The Megapodagrioninae

Here are included the genera ordinarily considered as belonging to the legion Podagrion of de Selys; this is the group which leads to the higher members of the Coenagrionidae. The genus most distinct from the others is undoubtedly *Thaumatoneura* (fig. 51), which has been given much attention by various workers. McLachlan (1897) and Foerster (1909) referred it to the Agrionidae; Needham (1903a) spoke of its affinities to the Pseudostigmatinae and Calvert (1913) placed it in the Megapodagrioninae. All agreed that it was an intermediate form. The safest course to follow seems to be to leave it in the Megapodagrioninae, but to call attention to the fact that it shows an undoubted approach to the Pseudostigmatinae. It is unquestionably one of the *Coenagrionidae* although it does have more than two antenodals. *Neurolestes* (fig. 62), *Trineuragrion* (fig. 54), and often *Neuragrion* have three antenodals as the normal condition, so that the old idea of

two as being an infallible means of determining Coenagrionidae must give way, as has been stated by previous workers. The retraction of the nodus is a more fundamental difference than the retention of four or five cross-veins and must place the genus in the higher family. Now as to its subfamily; it is convenient to limit the Pseudostigmatinae to those genera in which the stigma becomes diffused and which have M_{1a} following M_2 rather than M_1. If this is done, *Thaumatoneura* may be placed near the base of the *Pseudostigma* line. I can readily see, however, that its general vein-arrangement, its large postnodal area, its broad area behind Cu and its retracted nodus may indicate a condition near enough to that of *Megaloprepus* (fig. 46) to warrant placing the two in the same subfamily.

To return to the general discussion of the Megapodagrioninae, it may be said that *Rhipidolestes* (fig. 52) in the position of the base of M_3 shows a decided affinity to the *Lestinae*, to separate it from which is perhaps as artificial an arrangement as to divide *Thaumatoneura* from the Pseudostigmatinae. The extreme petiolation and long narrow quadrangle, however, of *Rhipidolestes* throw it in this subfamily, which may be said really to begin with *Podopteryx* (fig. 53). From there on, the adult venation at least, gives a well connected series which has been carefully discussed by Dr. Calvert (1913). As nearly as they can be made to do so the keys show my interpretation of its evolution. M_3 and R_s at their points of attachment move outward to beyond the subnodus, the quadrangle becomes elongate, the wing reaches the extreme of petiolation, and the number of supplementary sectors is reduced to none other than M_{1a}.

Tillyard (1914), on the basis of the presence of the oblique vein formed the Synlestinae as a group including such genera as *Chlorolestes* (fig. 66) and *Synlestes* (fig. 63), and placed them with the Lestinae. But, as has been shown, this was a dangerous undertaking. According to Schmidt (1915) the genera *Chlorolestes* (fig. 66) and *Synlestes* (fig. 63) belong to the *Lestinae* on the basis of the structure of the male genitalia; his figures, however, fail to show any very close connection. Venationally they are not to be placed in the Lestinae; M_3 arises very near to or at the subnodus although

the general wing proportions are those of the Lestinae, in which it arises far before the subnodus: petiolation has proceeded to the level of half the length of the quadrangle; in the Lestinae it does not reach the arculus. It is true that Cu_1 arches forward just beyond MA as in *Lestes* (fig. 44), but that is the case in some other genera as well; for example *Chorismagrion* (fig. 69) and *Trineuragrion* (fig. 54) and *Dimeragrion* (fig. 67) to a certain extent. *Rhipidolestes* (fig. 52) in its venation is nearer to *Lestes* (fig. 44), but Schmidt considers it much nearer *Megapodagrion* (fig. 57) itself on the basis of the penis.

I have spoken before of the progressive reduction of the sectors in the Megapodagrioninae until all except M_{1a} are gone; when this state is arrived at, the condition to be found in the Coenagrioninae is present. But there are two genera which agree with the Coenagrioninae in this respect, but which seem better retained in the Megapodagrioninae. These are *Chorismagrion* (fig. 69) and *Perilestes* (fig. 70); their extreme petiolation, the remote origin of R_s and M_3, the arching forward of Cu_1 beyond MA, and the heavy stigma of *Chorismagrion* are indicative of affinity to *Synlestes* (fig. 63) and *Heteragrion* (fig. 68) and through its likeness to *Chorismagrion, Perilestes* is to be placed at the apex of the *Megapodagrion* line.

Just the fact, then, of the presence or absence of supplementary sectors is not a safe criterion by which to separate the Megapodagrioninae from the higher forms. It is indeed an accompaniment of specialization and reduction and is a convenient character to use. Generally mere presence or absence is not so reliable a matter as might be supposed, since two forms without a given character may have arisen independently from two very distinct ancestors, one with the character present in one way, another with it in quite a different way.

It is probable, however, that the forms placed by de Selys in the legions *Agrion* and *Platycnemis* have been derived from others, closely related to *Megapodagrion* (fig. 57), in which petiolation has not reached the level of Ac and in which M_3 arises before the subnodus. A wing like that of *Megapodagrion* with the supplementary sectors removed would be much like *Platycnemis* (fig. 74). Perhaps the distinction between the legion *Podagrion* on the one hand,

and *Platycnemis* and *Coenagrion* on the other is hardly great enough to merit their being placed in separate subfamilies, but it may be done, if it is kept in mind that the groups are close to each other and that the second is an offshoot from the first.

So much may suffice for a discussion of the Megapodagrioninae; those groups to which it has given origin may now be discussed.

The Pseudostigmatinae

As here used, this subfamily includes the Anormostigmatini of Kirby's Catalogue, and is characterized by a diffusion of the stigma, by having M_{1a} parallel to M_2 rather than to M_1, and by a very retracted nodus with a long postnodal portion which has many cross-veins and with the longitudinal veins running far out into the wing. These insects are as specialized in a venational way as in their elongate abdomens and peculiar habit of life, the nymphs living in the small pools in epiphytic Bromeliads. If it were not for the genus *Thaumatoneura* (fig. 51) they would stand so far removed from all other Zygoptera as perhaps to deserve a separate family.

Megaloprepus (fig. 46), however, the most generalized of the five genera, has so many points of similarity to *Thaumatoneura* that there can be no doubt of their relationship. They agree in the width and general proportions of the wings, in the presence of abundant sectors and the position of the nodus. *Megaloprepus* shows a more generalized condition than the remaining genera in the short quadrangle, the broad area back of Cu_2 with many attached sectors, and in the fact that the stigma while diffuse is not so much so as in the others.

Within the group the same tendencies of specialization appear as in other groups: loss of sectors, narrowing of the wing, reduction in number of cross-veins, straightening of veins, elongation of the quadrangle, and petiolation of the wing. Next to *Megaloprepus* comes *Microstigma* (fig. 47), with the quadrangle about five times as long as wide and with M_{1+2} forking more than half the distance from the subnodus to the tip of the wing. In these respects these two genera differ from *Anomisma* (fig. 48), but agree with it in having many secondary sectors and with Cu_2 bearing many branches. *Anomisma* is peculiar in being a genus of Coenagrionidae having a crossed quadrangle, *Pseudostigma* (fig. 49) and *Mecistogaster* (fig.

50) have few sectors and no branches to Cu_2. *Mecistogaster* is the most specialized of all, with a single row of cells behind Cu_2 and between M_{1a} and M_2. It is interesting to note that in this group the tendency is for the nodus to approach a more normal position in the wing, so that in *Mecistogaster* (fig. 50) it is at one-fourth the length of the wing, while in *Megaloprepus* (fig. 46) it is at one-seventh.

The Coenagrioninae

Baron de Selys created two legions, *Platycnemis* and *Agrion*, for the reception of genera which fall, it is true, into two groups, but these have no definite nor sharply defined differences. In general it can be said that the quadrangle of the first of these groups has a relatively long upper side, hence that the outer angle is not very acute, but there are exceptions to this, as for example in *Leptocnemis* (fig. 80); in the second legion there are exceptions to the obliquity of the quadrangle, since some of the more specialized forms, as *Hemiphlebia* (fig. 106) and *Agriocnemis* (fig. 104), have a fairly regular one. For that reason a recent key to subfamilies of the Zygoptera does not hold as applied in the following quotation:

"Quadrilateral regular.....Subfamily *Platycneminae*.
Quadrilateral irregular, usually with distal angle sharply acute.
Subfamily *Agrioninae*."[3]

Now these two groups have many points in common; they have no supplementary sectors other than M_{1a}, they have the stigma rather short as compared with that of the Megapodagrioninae and they have Cu_2 well developed. Since they do grade so from one into the other, and are so fundamentally related, I cannot follow the above example and place them in separate subfamilies; in fact, I am not absolutely sure that as many such divisions ought to be recognized as I have already done in this paper, that is, whether these "subfamily" groups are really equivalent to subfamilies in other orders.

This placing both in one group does not indicate, however, that my feeling is that the legions *Platycnemis* and *Coenagrion* are not rather distinct. Although the quadrangle alone does not suffice in

[3] Agrioninae is here used for the legion Agrion of de Selys, hence it is equivalent to the Coenagrioninae of this paper minus the Platycnemis group.

all cases to separate the two, the general wing proportion and arrangement of the veins do. In *Platycnemis* (fig. 74) and its allies the wing is long and with the longitudinal veins arranged in a very regular and parallel fashion. The cells are largely square or rectangular, while in the group containing *Coenagrion* (fig. 94) there is a tendency for M_{1+2} to bend posteriorly at the subnodal region and for M_4 and Cu_2 to be zigzag so that many cells are pentagonal. The methods of specialization in the two groups are also different, in the *Platycnemis* series are retained some of the features to be found in the Megapodagrioninae; for example, (1) great petiolation which may extend beyond the level of the arculus, and (2) an outward migration of the base of R_s to a considerable distance beyond the subnodus. In the second group, on the other hand, petiolation is delayed for a long time, so that it never reaches the level of the arculus, and R_s arises beyond the subnodus in *Amphicnemis* (fig. 129) only. Many of the *Coenagrion* group are further specialized by a great reduction in the number of cross veins in the wing.

To come now to the discussion of the legion *Platycnemis* in detail, it is perhaps to be noted first of all that this may not be a natural group, it may represent a collection of forms each of which is the result of the dropping out of sectors from some corresponding Megapodagrionine. If *Megapodagrion* (fig. 57) itself, by way of example, were to lose its supplementary sectors, the resulting venation would be much like that of *Platycnemis* (fig. 74) or *Calicnemis* (fig. 72). The same might be true of *Wahnesia* (fig. 65) and *Tatocnemis* (fig. 78), of *Heteragrion* perhaps, (fig. 68) and of *Prionocnemis* (fig. 79). However this may be, and although these genera resembling *Platycnemis* may not have come from a common ancestor, they do form a remarkably close and well connected series beginning with *Metacnemis* (fig. 71), *Calicnemis* (fig. 72), and *Platycnemis* (fig. 74), in which the wing is not petioled to the level of Ac, and R_s begins at the subnodus. Proceeding through *Idiocnemis* (fig. 75), *Coeliccia* (fig. 76), and *Allocnemis* (fig. 77), petiolation and the outward movement of the base of R_s advance until the two tendencies reach their culmination in *Tatocnemis* (fig. 78) and *Prionocnemis* (fig. 79) respectively.

Leptocnemis (fig. 79) and *Paracnemis* which are rather typical forms of the *Platycnemis* group, except in the proportions of the quadrangle, and *Antiagrion* (fig. 81) a segregate of the old genus *Coenagrion* itself, offer themselves as transitional genera to the remaining Coenagrioninae.

These other genera in turn, can be divided into two groups: the *Argia* group and that of *Coenagrion* proper. In the former the inner end of the quadrangle is generally longer than the upper part of the arculus and as long as the upper side of the quadrangle, which is widened distally. Another character, not venational, is the presence of long tibial spines. This group has its own evolutionary line which begins with *Hyponeura* (fig. 82) and *Palaiargia* (fig. 83) and proceeds by greater petiolation, shortening of Cu_2, and reduction of the number of postnodals through *Argia* (fig. 84) to *Argiallagma* (fig. 86) and *Diargia* (fig. 85).

Of the *Coenagrion* group proper, it may be said that venation offers fewer marks for identification than in any other group of the Zygoptera, and it is here that keys for determination must be artificial. The genera are so numerous and so much alike that other characters are necessary for their differentiation. Venation does, however, indicate the general tendencies of phylogeny. Mr. Tillyard (1912) may be quoted as follows, "Those forms are the least asthenogenetic in which the basal postcostal nervule[4] is closest to the base of the wing, the petiolation consequently least marked, and the inferior sector of the triangle longest and best developed. Such forms, while marking the 'high-water mark' of successful coenogenetic specialisation in the legion, must nevertheless be considered to be more in line with the ancestral stem of the group than are their asthenogenetic off-shoots." Following this theory, one can readily arrange a series which begins with *Oreagrion* (fig. 87) and *Pyrrhosoma* (fig. 89) and, by a shortening of Cu_2 and a reduction in the number of postnodals, continues through *Enallagma* (fig. 98), *Ischnura* (fig. 100) and *Coenagrion* (fig. 94) to another dividing point, one branch leading off in the direction of reduction in size and further decrease in the number of postnodals until *Ceratura* (fig. 102), *Anomalagrion* (fig. 97), *Agriocnemis* (fig. 104)

[4] Basal postcostal nervule is the vein Ac of this paper. Inferior sector of the triangle is Cu_2.

and *Hemiphlebia* (fig. 106) are arrived at; the other branch develops by a greater petiolation, which extends to or beyond Ac in those genera above *Pseudagrion* (fig. 114). This line continues through *Oxyagrion* (fig. 109), *Acanthagrion* (fig. 110) and others until a new tendency is observable, namely the movement outward of the base of M_3, until the origin of this vein very nearly coincides with that of R_s. This is true of such genera as *Nesobasis*, *Aciagrion* (fig. 123), *Leptobasis* (fig. 127) and *Teinobasis* (fig. 128). In *Amphicnemis* (fig. 129) the base of M_3 reaches the subnodus and R_s arises a cell beyond, while petiolation extends at least to the level of the arculus.

To return for a moment to the discussion of *Ceratura* (fig. 102), *Anomalagrion* (fig. 97) and their allies; there are to be found here several very interesting and peculiar conditions. The male of *Anomalagrion hastatum* in the fore-wing has the stigma small and three-sided, with the apex of this triangle not reaching the margin of the wing, and with the base on R_1. *Ceratura* (fig. 102), *Austrocnemis* (fig. 104) and *Hemiphlebia* (fig. 106) have the second antenodals placed before the arculus, and have only from five to seven postnodals, while Cu_2 extends but a few cells beyond the level of the subnodus. In *Austrocnemis* and *Hemiphlebia* petiolation extends almost to Ac, since Ab and Ac are in line with each each other, A′ does not begin at the wing margin and the other characters above mentioned place these two genera in this line rather than in the *Leptobasis* one. The absence of the inner end of the quadrangle in the fore-wing of the male of *Hemiphlebia* (fig. 106) is an unusual state of affairs, and an interesting parallelism to the Megapodagrionine *Chorismagrion* (fig. 69) recently described by Morton (1914).

The Protoneurinae

This subfamily, the most specialized one among all the Zygoptera, includes the legion Protoneura of de Selys. It is distinguished primarily by the reduction in length of Cu_2 which is generally represented by a cross-vein only. In fact, this character was the one first used by de Selys to determine whether a genus belonged in the legion or not. On the discovery of *Proneura prolongata* (fig. 131), in 1889, with the vein Cu_2 one cell long, he modified the definition

of the legion to include this form and the genus *Chlorocnemis* (fig. 130) which is likewise characterized by having Cu_2 one cell in length. It is of course evident that these two genera are intermediate between the old legions Agrion and Platycnemis proper. Yet they are closer to the latter and may easily be considered as coming in the same subfamily with it.

Chlorocnemis (fig. 130) with its general wing proportions and arrangement of veins is a genus connecting *Platycnemis* (fig. 74) with such genera as *Palaemnema* (fig. 136) and *Platysticta*, which also have a long postnodal area with the longitudinal veins very regularly and evenly placed. *Proneura* (fig. 131), on the other hand, shows its affinities with the *Coenagrion* group on the one side and *Neoneura* (fig. 133) and related genera on the other, in it are found the pentagonal cells near M_4, the bend of M_{1+2+3} before the subnodus, and the small number of the cells of the wing and a short vein M_{1a}.

After Cu_2 has become reduced, the next step in the evolution of the *Protoneurinae* seems to have been the atrophy of that part of the anal vein beyond Ac. Thus in *Disparoneura* (fig. 132), *Peristicta* (fig. 134), *Neoneura* (fig. 133), and *Idioneura* (fig. 135) it extends to the medio-anal link; in *Palaemnema* (fig. 136) and the old genus *Platysticta* (fig. 137) it ends before MA on the posterior edge of the quadrangle, and in *Hypostrophoneura* on the hind margin of the wing. In the higher forms it does not extend beyond Ac, which then is generally moved nearer the base of the wing until in *Nosticta* (fig. 151), *Isosticta* (fig. 150), and *Selysioneura* (fig. 153) it lies before the level of the first antenodals. At the same time Cu_1 becomes shorter and the whole line culminates in *Selysioneura* (fig. 153), which has only a cross-vein for both Cu_1 and Cu_2. In its absence of sectors other than M_{1a}, in the reduction of Cu_1 and Cu_2, in the origin of both R_s and M_3 beyond the subnodus, in the absence of that portion of A beyond Ac, in the retracted position of Ac, and in the fact that the second antenodals lie before the arculus, this genus presents a combination of characters of so high a degree of specialization that it can hardly be equalled in its reduction by any other member of the Zygoptera. It is therefore fitting that it should be placed at the very apex of the genealogic

tree of the suborder, and should bear the name of the man who has done more than any other worker to further our knowledge of the Odonata, namely Baron de Selys-Longchamps.

In contrast to the Coenagrioninae the Protoneurinae do not have the reduction in the number of postnodals, they are as numerous in *Selysioneura* (fig. 153) as in *Disparoneura* (fig. 132).

III—TENDENCIES IN SPECIALIZATION

These have been rather fully discussed in previous papers, particularly by Dr. Needham (1903a) for the order Odonata as a whole, and by Dr. Calvert (1913) for the Zygoptera with special reference to the Megapodagrioninae. It is my purpose here to review their opinions and to add a few observations of my own.

I think it must be apparent from the preceding discussion on the phylogeny that the outstanding features in the development of the Zygoptera are a constant reduction and simplification of venation. At any rate this is true from the standpoint of comparative morphology and to a certain degree it seems to be so paleontologically. As might be expected this reduction is to some extent accompanied by a decrease in the power of flight. Dr. Calvert says, "Many of the ideas which have been expressed on the changes which have taken place in the venation of the Odonate wings have been based on the comparative morphology of living representatives of the order or on mechanical advantage. It does not follow that these foundations are trustworthy or that there has always been mechanical improvement in the wings. Degeneration is just as probable as progressive development. The actual course of phylogeny cannot be deduced from these considerations or from the data of morphology. It seems therefore desirable to attempt to ascertain what paleontological evidence exists affording clues to the descent of these insects, by tracing the modifications which the wings exhibit from the Carboniferous period down to the present time." This is what he has done and free use is here made of his conclusions.

It should be noted that the tendencies here discussed are not all present in the group, nor all to be found even in the highest groups, but they are those which impress one, when studying over all the groups, as being indicative of advancement and departure from the

generalized condition. They fall under two or three general heads and may be so treated in their discussion. First come those which may be classified under "Vein Reduction," secondly, those having to do with "Vein Shifting," and as a last group "Miscellaneous Features."

Vein Reduction

1. *Reduction in the number of supplementary sectors.*—This is one of the most evident means of specialization within any group which possesses such sectors, as well as in the whole suborder, of which the two highest subfamilies have none. A comparison of the different subfamilies in this regard may be made in a general way by choosing for each one as its most typical genus the one after which it is named. In Table I this has been done, the figures indicating the number of sectors between the veins listed at the top of the columns. The figures are for the front wings.

Table I

The Number of Supplementary Sectors present in the Subfamilies of Zygoptera

Subfamily	Genus and Species	M_1–M_{1a}	M_{1a}–M_2	M_2–R_S	R_S–M_3	M_3–M_4	M_4–Cu_1	Cu_1–Cu_2	Cu_2 Margin	Total
Polythorinae	*Polythore gigantea*	0	4	0	3	7	2	5	2	23
Agrioninae	*Agrion virgo*	7	2	2	7	8	8	3	8	45
Epallaginae	*Epallage fatima*	5	2	2	3	4	4	4	4	28
Disparocyphinae	*Disparocypha biedermanni*	2	2	2	2	0	0	0	0	8
Megapodagrioninae	*Megapodagrion erinys*	0	2	2	0	1	0	0	0	5
Lestinae	*Lestes rectangularis*	0	2	2	2	3	0	0	0	9
Lestoidinae	*Lestoidea conjuncta*	2	0	0	0	0	0	0	0	2
Pseudostigmatinae	*Pseudostigma aberrans*	2	1	1	1	1	1	0	1	8
Coenagrioninae	*Coenagrion puella*	0	0	0	0	0	0	0	0	0
Protoneurinae	*Protoneura capillaris*	0	0	0	0	0	0	0	0	0

It should be remembered of course that such a table is of value in a general way only, since there is great variation in some subfamilies. *Epiophlebia* is a member of a lower suborder, yet its supplementary sectors are not so numerous as those of many Zygoptera. *Thaumatoneura* (fig. 51) is placed in the Megapodagrioninae, but its many sectors indicate a primitive condition, or possibly they may represent a secondary acquirement. Nevertheless, this table shows that the highest subfamilies have the fewest sectors.

Dr. Calvert has shown that in a general way the reticulation of the oldest fossil order related to Odonata, the Protodonata, was rich in supplementary sectors. In Anisozygoptera some wings were richly veined, others less so. He concludes, that we have, therefore, "only the general tendency to guide us when we assume that reduction in density of venation means specialization."

2. *Reduction of the veins* Cu_2 *and* Cu_1.—This tendency appears in three widely removed groups; by it are derived *Disparocypha* (fig. 37) from the *Epallaginae*, *Lestoidea* (fig. 45) from the Lestinae, and the Protoneurinae from the Coenagrioninae. As was shown in the discussion of the Protoneurinae, Cu_1 follows Cu_2 in its reduction until nothing remains for both except the cross vein forming the lower part of the medio-anal link. This condition is the one to be found in *Selysioneura* (fig. 153) and is approached by a number of forms, such as *Nososticta* (fig. 151) and *Isosticta* (fig. 150).

3. *Decrease in the number of antenodal cross-veins.*—This very apparent tendency needs but little discussion, particularly after the thorough treatment given it by Campion (1913). The number of cross-veins in the lower Agrionidae is very high; in the higher Epallaginae it is reduced to seven, eight, and nine; in the Coenagrionidae, only *Thaumatoneura* (fig. 51) has over three. *Neurolestes* (fig. 62), *Trineuragrion* (fig. 54), and *Neuragrion* have three generally, in one wing at least; and *Chlorolestes* (fig. 66), *Podopteryx* (fig. 53), *Paraphlebia* (fig. 64), *Heteragrion* (fig. 68), and *Pyrrhosoma* (fig. 89) have occasionally been observed to have three; all others commonly two. Dr. Calvert cites evidence to show that this reduction is not in proportion with the retraction of the nodus, but is apparently an independent and recent acquisition.

4. *Decrease in the number of postnodals.*—In the Zygoptera this tendency comes in much later than does the reduction in the antenodal series, nor does it ever reach so advanced a state. It appears very marked in the Coenagrioninae only, and there in the *Argia* and *Coenagrion* series some of the highest genera such as *Diargia* (fig. 85), *Agriocnemis* (fig. 104), *Hemiphlebia* (fig. 106), and others have very few postnodals.

5. *Loss of the cross-veins in the quadrangle and subquadrangle.*—The number of cross-veins in and before the subquadrangle seems generally to correspond roughly to that of the antenodals. In those Agrionidae with numerous antenodals the subquadrangle is generally crossed and the number of "cubito-anal" cross-veins is so great that Ac itself is distinguished only with difficulty. *Neocharis* (fig. 31) offers an interesting exception; in it the antenodals of both series are numerous, but there are no true cross-veins back of Cu. *Diphlebia* (fig. 34) and *Amphipteryx* (fig. 35) may also have none. In the Coenagrionidae the lack of cross-veins in the subquadrangle has become the normal state and it is only in such forms as *Paraphlebia* (fig. 64) and *Dimeragrion* (fig. 67) that any are found. The same tendency is true of the cross-veins of the quadrangle; they are first lost in the Epallaginae and in the higher forms are normally retained by one genus only, *Anomisma* (fig. 48).

6. *Reduction in number of those antenodal cells situated between M_4 and Cu_1.*—As shown by Dr. Calvert "this character is in general dependent on the degree of retraction of the nodus," and, "a reduction in the number of antenodal cells may occur independently of retraction of the nodus, however, by the greater development of the quadrilateral distad." It is evident also that this reduction is a part of the general tendency toward a smaller number of cross-veins in the wing as a whole; almost any part of which when observed through a long ascending series, will show the cross-veins becoming placed further apart. Other examples of the tendency might be noted, for instance, the freeing of the basal radial space where the latter exists.

7. *Reduction in the number of cross-veins behind the anal vein.*—In part this is in line with the general tendency to drop out cross-veins; in part due to progressive petiolation which reduces the

amount of space back of the anal bridge and therefore the possibility of cross-veins occurring there.

Vein Shifting

1. *Narrowing of the wing.*—This tendency is coupled with the first one mentioned in the previous group, namely the reduction in the number of sectors. When the sectors drop out, the principal veins come to lie closer together. The wing may become narrower also by the veins Cu_1 and Cu_2 becoming reduced. A comparison of the typical genera of the subfamilies shows at a glance how prevalent this tendency is (see Table II).

Table II

The Ratio of the Width of the Wing to the Length in the Different Subfamilies.

Subfamily	Typical genus and species	Ratio, as Decimal
Polythorinae	*Polythore gigantea*	.380
Agrioninae	*Agrion maculatum*	.345
Epallaginae	*Epallage fatima*	.228
Disparocyphinae	*Diparocypha biedermanni*	.167
Megapodagrioninae	*Megapodagrion erinys*	.201
Lestinae	*Lestes rectangularis*	.203
Lestoidinae	*Lestoidea conjuncta*	.252
Pseudostigmatinae	*Pseudostigma, sp ?*	.195
Coenagrioninae	*Coenagrion resolutum*	.210
Protoneurinae	*Protoneura capillaris*	.152

It is evident in this table, what effect the dropping out of Cu_2 in *Disparocypha* and *Protoneura* has on the width of the wing. In *Lestoidea*, however, the presence of two sectors between M_1 and M_{1a}, has offset this tendency (see fig. 45).

The Pseudostigmatinae is a good example of the same tendency (see Table III). The subfamilies Megapodagrioninae, Coenagrioninae, and Epallaginae might be used for similar tables.

An examination of Handlirsch's figures in "Die Fossilen Insecten" show some rather narrow wings in periods as remote as the Mesozoic; evidently narrowing of the wing and loss of the sectors are ancient tendencies.

Table III

The Ratio of the Width of the Wing to the Length, in the Pseudostigmatinae.

Genus and Typical Species	Ratio, as Decimal
Megaloprepus coeruleatus	.267
Microstigma exustum	.237
Anomisma abnorme	.204
Pseudostigma aberrans	.177
Mecistogaster marchali	.148

2. *Progressive petiolation.*—In each subfamily except the Agrioninae, where specialization is along a different direction, there is a very noticeable tendency toward greater petiolation; it has been referred to constantly in the discussion on phylogeny and is used often in the keys, offering as it does an easy index to the amount of departure from the primitive. The Protoneurinae might be considered an exception, since in them, A becomes shorter and the reduction process is a matter of retraction. But in both cases the result is the narrowing of the wing near the base. Dr. Calvert discusses petiolation from the paleontological standpoint and says, "It seems justifiable to assume that the farther distad petiolation has progressed, the more specialized the insect."

Petiolation reaches its highest development in the Megapodagrioninae where in *Chorismagrion* (fig. 69) and *Perilestes* (fig. 70) it extends to beyond the level of MA.

3. *Retraction of the nodus toward the wing base.*—This is one of the most common and evident occurrences in specialization and is discussed in detail by both Professors Needham and Calvert. In the Agrionidae the nodus is almost universally at more than one-third the distance from the base of the wing toward the tip, in the Coenagrionidae at generally less.

4. *Tendency for M_2, R_s, and M_3 to arise nearer the tip of the wing and further from the subnodus.*—As Dr. Calvert remarks this outward "migration may be real or apparent. Retraction of the nodus with no change in position of the separation point of M_2 would result in a greater interval between nodus and M_2 and hence an apparent movement of the latter toward the stigma, but no real movement in respect to the wing as a whole." His table for

various members of the Megapodagrioninae shows it is often apparent only; but even if so a combination of the preceding tendency and of this one indicates specialization.

A study of almost any group will show the same thing; one that is a good example is the *Platycnemis* group of the Coenagrioninae (see Table IV).

Table IV

The Ratio to the Length of the Wing of the Distance from the Base of the Wing to the Subnodus and Points of Origin of M_2, R_s, and M_3.

Genus and Species	Subnodus	M_2	R_S	M_3
Metacnemis valida	.381	.619	.381	.362
Calicnemis eximia	.309	.576	.309	.289
Psilocnemis marginipes	.354	.631	.354	.339
Platycnemis pennipes	.354	.562	.354	.323
Allocnemis leucosticta	.345	.582	.345	.322
Coeliccia membranipes	.311	.613	.311	.301
Tatocnemis malgassica	.311	.561	.327	.311
Prionocnemis haematopus	.191	.591	.435	.209

A first glance at the wings themselves might suggest to one that M_2, R_s, and M_3 arise further out in the wing in the last genera than in the first, but an inspection of the above table shows that in general this is not true. It is not even equally true of the different veins but may be more so of some than others; R_s for example in *Prionocnemis* (fig. 79) does arise beyond what it does in the others, M_2 and M_3 really arise nearer the base in the more specialized than in the lower wings. The subnodus becomes more retracted, quite consistently so, and the space between it and the points of origin of M_2 and R_s enlarges, while the relative positions of the subnodus and the base of M_3 change.

A comparison of the Agrionidae and of the Coenagrionidae shows on the whole, that in the lower subfamilies of the latter family the vein M_{1+2} forks at about one-half the wing-length, as it does in the former family, but in the higher subfamilies the movement outward is evident. In the whole series R_s and M_3 also migrate outward. Dr. Calvert says that "the paleontological evidence is not altogether satisfactory and at least admits of the possibility of the separation—points of these three veins having fluctuated proximad or distad from time to time."

5. *Migration outward of the base of* M_{1a}.—This tendency is correlated somewhat with the preceding, but seems to be independent of it to a certain degree. Most genera among the Agrionidae, Pseudostigmatinae, Lestinae, and Megapodagrioninae have M_{1a} arising about three or four cells beyond the fork of M_{1+2}, or at least rather near it. *Perilestes*, (fig. 70) however, which has M_{1+2} forking about two-thirds of the way out has M_{1a} arising below the outer end of the stigma, or about one-fourth of the wing-length beyond M_2. This is true to a lesser degree in some of the Coenagrioninae such as *Platycnemis* (fig. 74), *Antiagrion* (fig. 81), *Hyponeura* (fig. 82), *Agriocnemis* (fig. 104), *Ceriagrion* (fig. 117) and others. It is not on the whole an important character, but does occasionally seem worthy of notice.

6. *The position of the second antenodals before the arculus.*—In those Agrionidae with many antenodals, there is a tendency for two of the costal antenodals to become more strongly developed than the others, and to be in line with two corresponding ones of the subcostal series, while at the same time the second of these pairs is directly above the arculus. In *Epiophlebia* (fig. 1) this second pair lies considerably beyond the level of the arculus; in *Polythore* (fig. 2) and *Euthore* (fig. 3) it is at that level, in *Cora* (fig. 5) and *Chalcopteryx* (fig. 4) before it. In the Agrioninae, i.e. the legion *Calopteryx*, there is no evident hypertrophy of antenodals, but in the Epallaginae the tendency is again evident and the number of antenodals is reduced, until the two pair typical of the Coenagrionidae remain. Here, as in the Polythorinae and some Epallaginae, in some of the most highly developed forms: *Lestoidea* (fig. 45), *Perilestes* (fig. 70), *Chorismagrion* (fig. 69), *Ceratura* (fig. 102), *Agriocnemis* (fig. 104), *Hemiphlebia* (fig. 106), *Caconeura* (fig. 143), *Protoneura* (fig. 146), *Selysioneura* (fig. 153) and others, the second antenodals are distinctly before the level of the arculus. Since this tendency rarely is manifest except in the highest members of the respective groups, it seems indicative of specialization.

7. *The tendency for the quadrangle to become acute distally.*—Dr. Needham (1903a) has taken as the primitive type of quadrangle one square distally and Mr. Williamson (1913) agrees that "in the relations of MA," the Calopteryginae (Agrionidae of this paper)

shows a generalized structure and adds that for the Agrioninae (Coenagrionidae here) he believes in two lines of evolutionary activity, one in which MA is the center of activity and the quadrangle becomes pointed; the other in which MA is not changed, but the posterior area of the wing is reduced; here he refers of course to the Protoneurinae. Dr. Calvert (1913) disagrees with the views above expressed, partly because he finds no paleontological evidence for their support. He argues that since "all the Jurassic fossils, which are not clearly Anisoptera, show an oblique quadrilateral with its posterior distal angle acute," it seems "necessary to regard the oblique quadrilateral as the more primitive and the rectangular as a later appearance." It is true that the Anisozygoptera figured by Handlirsch have a quadrangle which is somewhat acute distally, and that the only living representative of this suborder, *Epiophlebia*, (fig. 10) has an acute quadrangle, so that this condition seems the more ancient. When the living Zygoptera are taken up, however, those that are in other respects the most primitive have the quadrangle regular; in the Agrionidae, it is only in the higher Epallaginae that the obliquity becomes noticeable; and in the higher Megapodagrioninae, Lestinae, Pseudostigmatinae, and those Coenagrioninae of the *Argia* and *Coenagrion* groups it is carried to its highest development. Comparative morphology, therefore, brings evidence to show that the obliquity of the distal end of the quadrangle is not a direct heritage from the Anisozygoptera, but rather by a parallelism or independent development, and in general is a sign of specialization.

I think that enough evidence has now accumulated to show that this obliquity may in turn, grow less and the quadrangle be restored to distal squareness. In other words, the quadrangle is not as fixed and unchangeable a part of the wing as might at first be supposed. How else can the same shape of the quadrangle be explained in three widely separate groups which agree only in the reduction of Cu_2? I refer to *Disparocypha* (fig. 37), *Lestoidea* (fig. 45), and the Protoneurinae. Evidently when this reduction takes place new demands for bracing must be met and the quadrangle again becomes square. The squareness of the quadrangle, then, in the lower Agrionidae and in the Protoneurinae, is no proof of a

primitive or of a specialized state in both groups, but of one in the first, and of the other in the second.

8. *Change in length of the quadrangle.*—At first thought the elongation of the quadrangle seems to be a tendency which may point to departure from the ancient condition and which occurs rather often. Further investigation, however, fails to permit of the selection of any very well marked series in which this can be traced. Apparent elongation may be due to narrowing of the quadrangle itself or retraction of the nodus so that the quadrangle almost reaches its level. Beginning with *Climacobasis* (fig. 6) and *Echo* (fig. 7) and proceeding to *Psolodesmus* (fig. 16), one can observe some elongation, and likewise with *Pseudophaea* (fig. 21), *Dysphaea* (fig. 22), *Anisopleura* (fig. 25) and *Rhinocypha* (fig. 26), and in some Megapodagrioninae the tendency is similar. But for the whole suborder it has perhaps been rather different; the highest Coenagrionidae have almost as short a quadrangle as *Pseudophaea* (fig. 21), in fact often they may seem to have a smaller one, partly because of distal obliquity and the resulting shortness of the upper side. The length of the quadrangle, then, does not greatly change, except in short series.

9. *Attachment of supplementary sectors.*—Here again is a tendency not at all universal in its appearance, but occuring often enough to deserve mention. Among the *Polythorinae* it is evident in *Chalcopteryx* (fig. 4); among the Agrioninae it begins in *Neurobasis* (fig. 14) and *Phaon* (fig. 17) and ends in *Vestalis* (fig 18); in the Coenagrionidae, *Thaumatoneura* (fig. 51) exhibits it to a certain degree, *Megaloprepus* (fig. 46), *Microstigma* (fig. 47) and *Anomisma* (fig. 48) to a higher one, but since in *Pseudostigma* (fig. 49) and *Mecistogaster* (fig. 50) almost all secondary sectors drop out, the tendency cannot longer manifest itself; nor can it in the Coenagrioninae.

10. *Straightening of the longitudinal veins.*—Wherever there are many supplementary sectors present, the principal veins tend to curve, especially near the margin of the wing. But when these sectors drop out the veins themselves become straight and scarcely curve. Among the Agrionidae, this is true of *Micromerus* (fig. 28) and *Philoganga;* among the Coenagrionidae of *Lestes* (fig. 44),

Mecistogaster (fig. 50), the higher Megapodagrioninae, and the Coenagrioninae and Protoneurinae generally. I think fossil evidence bears out this tendency equally well; it is, as was said above, apparently one dependent on reduction in the number of sectors.

11. *Matching up of the cross-veins in transverse series.*—At the same time that the preceding tendency becomes evident and, largely in the same forms, it is very noticeable that the cross-veins become matched up and form regular transverse series across the wing. These are beautifully illustrated in the higher Pseudostigmatinae, the Coenagrioninae and the Protoneurinae above all others.

Miscellaneous Features

1. *Differentiation of fore and hind wings.*—This tendency so important among the Anisoptera has practically no place among the Zygoptera. A marked difference in size and shape is noticeable in only very few cases: *Chalcopteryx* (fig. 4) among the Polythorinae, *Pseudolestes* (fig. 38) among the Lestinae, and sometimes *Mecistogaster* (fig. 50) among the Pseudostigmatinae. These cases are certainly evidence of a departure from the primitive condition.

Many Zygoptera have a fairly constant difference in the length of the quadrangles of the fore and hind wings, enough so that one can tell which is the front and which the hind wing. The Polythorinae have this difference well developed in that the quadrangle of the fore wing is much the shorter and with fewer cross-veins. Among the Coenagrionidae several subfamilies have the upper side of the quadrangle of the fore wing shorter than that of the hind wing. But, generally speaking, the differentiation of fore and hind wings among the Zygoptera is not of enough importance for it to be considered a sign of specialization.

2. *The bracing of the stigma.*—Dr. Needham has shown two ways by which this may proceed, one by the cross-vein between R_1 and M_1 below the inner end of the stigma becoming oblique and often hypertrophied. This sort of bracing is not met with in the Agrionidae, nor in the lower Lestinae nor Megapodagrioninae. In most higher Lestinae, Megapodagrioninae, Coenagrioninae, and Protoneurinae it is the usual thing. The plates in Handlirsch's "Die fossilen Insecten" show bracing in *Tarsophlebia*, a genus

of the Anisozygoptera and among the possible ancestors of the Zygoptera.

The other method of bracing is for the inner end of the stigma to be pointed and form a Y, the base of which is made by that portion of R_1 situated just before it. In this way R_1 holds the stigma firmly. Both methods may occur in the same wing. The Polythorinae have this Y well developed.

3. *Atrophy of the stigma.*—The diffusion and even total disappearance of the stigma in genera of two subfamilies, the Agrioninae and Pseudostigmatinae, may not be considered by some as a sign of advancement, but since the Odonata as far back as the Mesozoic do have the stigma, and since the modern genera which stand at the base of the Agrionine and Pseudostigmatine lines have it, and its gradual disappearance is traceable in a series, its atrophy must be taken as a matter of specialization, if not necessarily one of advantage.

IV—SUMMARY

From the preceding discussion it is evident that venation gives in most cases an easy and fairly clear means of determining relationships, but in certain ones it may be capable of more than one method of interpretation, and must therefore be checked up by other characters if a final decision is to be reached. Sometimes this doubtful condition is due to parallelism, sometimes to contradictory evidence from several sources; one character in the wing may indicate one tendency, another quite a different one.

The keynote to the phylogeny of the Zygoptera as based on venation is reduction. With this in mind one can divide the suborder into two families, the lower of which, the Agrionidae, has as lateral offshoots: (1) the Polythorinae (figs. 2–5) in which M_4 does not descend the arculus and the quadrangle is therefore broad at the base and concave above; (2) the Agrioninae (figs. 6–20), where the wing fails to become petiolated, but the stigma atrophies and the quadrangle becomes somewhat convex above and widened distally; and (3) at a much higher level, the Disparocyphinae (fig. 37) as a direct offshoot of the main line of descent, by a shortening of Cu_2, until it is represented by a cross-vein only. This main line of descent is to be found in the Epallaginae (figs. 21–36) which

advance by petiolation, by reduction of the number of cross-veins, especially of the antenodals, and by a retraction of the nodus toward the wing-base. The Epallaginae lead to the second family, the Coenagrionidae, with which they are connected by various intermediate forms: *Diphlebia* (fig. 34), *Philoganga* (fig. 36), *Thaumatoneura* (fig. 51), *Ortholestes* (fig. 39) and *Pentaphlebia*. Early in the Coenagrionidae the nodus becomes more retracted, the number of antenodals becomes established as two, and the number of supplementary sectors shows a decided tendency to be decreased. There are two general lines of descent as regards the points of origin of R_s and M_3; in the first one these veins retain the condition of the Agrionidae and arise nearer the arculus than the subnodus; this is true of the Lestinae (fig. 38–44) and Lestoidinae (fig. 45). In the Lestinae is developed a quadrangle which is acute distally, and in the other subfamily the vein Cu_2 is again reduced so that it does not extend beyond MA. The other line in the Coenagrionidae has R_s and M_3 migrate outward so that they arise nearer the subnodus than the arculus. The Pseudostigmatinae (figs. 46–50) are an immediate offshoot, with greatly elongated wings in which the nodus is retracted and the stigma becomes diffuse. The Megapodagrioninae (figs. 51–70) form the central branch which leads to the Coenagrioninae (figs. 71–129) by the loss of all sectors except M_{1a}, and also continues in its own direction by greater petiolation and outward progression of the base of M_3. The Coenagrioninae are also characterized by a slight movement outward of M_3 and by a great reduction in the number of postnodals; petiolation on the whole does not proceed very far. This family in turn gives rise to the Protoneurinae (figs. 130–153) by the reduction of Cu_2, a change which has thus taken place in three groups of Zygoptera. In the Protoneurinae Cu_1 also becomes short, and in the highest form, *Selysioneura* (fig. 153), Cu does not branch at all.

V—KEYS FOR THE DETERMINATION OF GENERA

For the most part these keys indicate as nearly as they can be made to do so, the same views regarding the phylogeny of the Zygoptera as have been expressed in the preceding pages. The Coenagrioninae have been the stumbling block for such a system,

and although an arrangement can be made which seems to follow the general line of descent in this subfamily, and to indicate what tendencies have been followed out venationally, it has been so far impossible to base any key on venation, since the genera as now recognized have considerable variation within themselves. It has been necessary, therefore, to make use of structural characters for this subfamily, and to make a key for which no claims of natural relationship can be made, but which is merely an attempt to aid in identification. Before this difficult group can be finally worked out, however, much more material must be studied than it has been possible to study for this paper.

The nomenclature of veins used in the keys is the same as that shown in the wings of *Agrion* and *Argiocnemis* in the first part of the paper. The number of the figure appearing in connection with each genus refers to the plates at the end of the paper. For the following genera neither figures nor specimens have been available: *Paraphaea*, *Caliphaea*, and *Pentaphlebia* among the Agrionidae; and *Orolestes*, *Platylestes*, *Protolestes*, *Mesopodagrion*, *Metagrion*, *Allolestes*, *Argiagrion*, *Heteropodagrion*, *Mesagrion*, *Mesocnemis*, *Mombagrion*, *Myagrion*, *Nesocnemis*, *Nesobasis*, *Neuragrion*, *Onychargia*, *Paracnemis*, *Pericnemis*, *Phasmoneura*, *Stenocnemis*, and *Thermagrion* among the Coenagrionidae.

The material used for study of the other genera was that in the collections at Cornell University, at the Academy of Natural Sciences at Philadelphia, at the National Museum, in the private collection of Mr. C. H. Kennedy, and some borrowed from Mr. E. B. Williamson, the Carnegie Museum, and the Museum of Comparative Zoology. In addition to this free use was made of those figures and keys which appear in the literature, and of some photographs sent by Mr. H. Campion of the British Museum.

Key to the Suborders of Odonata

1 (4). Fore and hind wings essentially similar; in repose, held vertically or half-opened; eyes far apart. A quadrangle present. Males with two superior and two inferior abdominal appendages. 2

2 (3). Area between M_4 and Cu_1 just beyond MA as broad as that between Cu_1 and posterior margin of the wing. Quadrangle of hind wing and that of fore wing quite different in shape, the former twice as wide distally as proximally. Sectors of the wing (except M_{1a}) zigzag. . . . . **ANISOZYGOPTERA** (p. 40)

3 (2). Area between M_4 and Cu_1 just beyond MA generally narrower than that between Cu_1 and the posterior margin of the wing. The quadrangle of the fore wing of the same general shape as that of the hind wing; one may be longer than the other, but if one is widened distally, both are. Sectors of the wing tend usually to be continuous veins, not broken nor zigzag.

ZYGOPTERA (p. 40)

4 (1). Fore and hind wings dissimilar, held horizontally in repose. Eyes close together. Supertriangle and triangle present. Males with two superior and one inferior abdominal appendage.....**ANISOPTERA**[5]

Key to the Suborder Anisozygoptera

Family *Epiophlebiidae*. Subfamily *Epiophlebiinae*.

1. But one living genus. Characters those of the suborder. Japan and Eastern Asia. (Fig. 1).....**Epiophlebia** Calvert, 1903
(*Palaeophlebia* Selys, 1899)

Key to the Families and Subfamilies of the Suborder Zygoptera

1 (8). Antenodal cross-veins 5 or more. Usually cross-veins present in the subquadrangle beyond the vein Ac. M_3 separating from M_{1+2} nearer to the arculus than to the subnodus. Nodus usually more than one-third of the distance from the base of the wing to the tip. The quadrangle often crossed.
(Family **Agrionidae**).....2

2 (3). M not descending the arculus; quadrangle therefore concave anteriorly and at least twice as wide proximally as distally. Basal space crossed. Wings petioled at least one-half way to the arculus. M_{1a} closely parallel to M_1.

Polythorinae (p. 42)

3 (2). M descending the arculus for some distance; the quadrangle not markedly concave anteriorly, and not twice as wide proximally as distally, at least in the hind wing. Basal space crossed or not. Wings petioled or not.....4

4 (5). M_{1a} parallel to M_2. Stigma often atrophied. Quadrangle elongate, often as long as the basal space, and convex anteriorly. Cu_2 beyond the quadrangle, especially in the hind wing, sends off a branch (Cu_{2a}) to support the area posterior to it, or Cu_2 itself bends back to support this area.....**Agrioninae** (p. 42)

5 (4). M_{1a} not parallel to M_2, but more or less intermediate between M_1 and M_2 (not in *Micromerus*) and with rather prominent sectors on either side. Stigma well developed, at least in the hind wing. Quadrangle not so long as the basal space, or if so, not generally convex anteriorly. Cu_{2a} not present.....6

6 (7). Cu_1 and Cu_2 well developed veins, A extending as far as the distal end of the quadrangle. M_4 generally somewhat curved beyond MA. Stigma usually not much broader distally than proximally.....**Epallaginae** (p. 45)

7 (6). Cu_1 short, not reaching the level of the subnodus. Cu_2 reduced to a cross-vein. A following the hind margin of the wing beyond Ac for some distance, then bending forward and ending at the posterior side of the quadrangle. M_4 not curved beyond MA. Stigma much broader distally than proximally.

Disparocyphinae (p. 47)

[5] Not further discussed in this paper.

8 (1). Antenodals generally two, rarely three to five. Usually no cross-veins in the subquadrangle beyond Ac. M_3 separating from M_{1+2} nearer the subnodus than the arculus, except in the *Lestinae*, none of which have more than two antenodals. Nodus usually from one-fifth to one-third of the distance from the base of the wing to the tip. The quadrangle crossed in *Anomisma* only.
(Family **Coenagrionidae**) 9

9 (12). M_3 arising nearer the arculus than the subnodus. The base of R_s (properly, the base of the bridge to R_s) arising before the subnodus and generally as near the arculus as the subnodus 10

10 (11). Supplementary sectors present between R_s and M_3, and between M_3 and M_4. Cu_1 and Cu_2 well developed, extending considerably beyond the subnodus.
Lestinae (p. 48)

11 (10). No supplementary sectors between R_s and M_3, and between M_3 and M_4; two between M_1 and M_{1a}. Cu_1 one cell long and not reaching the subnodus. Cu_2 reduced to a cross-vein ..... **Lestoidinae** (p. 49)

12 (9). M_3 arising nearer the subnodus than the arculus (half-way in *Rhipidolestes*). The bridge to R_s short, arising at or beyond the subnodus (slightly before in *Rhipidolestes*) 13

13 (18). Cu_2 not reduced to a vein one cell long nor lacking 14

14 (15). Stigma diffused or lost, not made up of one cell, but if present, usually of several cells, and irregular in shape, not braced. The longest vein between M_1 and M_2 rather more parallel to M_2 than to M_1. Nodus at from one-fourth to one-seventh the wing length. Many postnodal cross-veins.
Pseudostigmatinae (p. 49)

15 (14). A true stigma present, usually braced at the inner end. M_{1a} not usually parallel to M_2, when any other sectors are present. Nodus generally at more than one-fourth of the wing length. The number of postnodal cross-veins often reduced 16

16 (17). Definite supplementary sectors present other than M_{1a} and arising at least as far in the wing as under the stigma. (No such sectors in *Chorismagrion* or *Perilestes*, but these genera can be recognized by the petiolation of the wing which extends almost to the level of MA, by the quadrangle coming near to the posterior wing-margin, by the arching of Cu_1 beyond MA, and by R_s arising several cells beyond the subnodus.) The stigma generally rather heavy.
Megapodagrioninae (p. 50)

17 (16). No definite supplementary sectors other than M_{1a} are present, except occasional very irregular ones which are only a few cells long and do not arise more than a few cells from the wing-margin. Stigma generally rather small.
Coenagrioninae (p. 53)

18 (13). Cu_2 reduced to a cross-vein, ending in the margin of the wing, or in two genera to a vein one cell long ..... **Protoneurinae** (p. 63)

Key to the Genera of the Subfamily Polythorinae

1 (8). Cu_2 branched, more than one row of cells between Cu_1 and Cu_2 and between Cu_2 and the wing-margin.....2

2 (7). Quadrangle of hind-wing one and one-half to two times as long as that of the fore-wing. Wings petioled about one-half of the way to the arculus. Fore-wing about three and one-half times as long as broad. Cu_2 forking, with two rows of cells between the branches. Arculus at slightly more than one-third of the distance from the base of the wing to the subnodus.....3

3 (6). Fore and hind wings of same general shape and size. Sectors arising between the main veins, which do not appear forked. M_2 arising within a cell or two of the subnodus.....4

4 (5). Venation very complex, many sectors and cross-veins; for example, 40–50 antenodals; often 12 or more cross-veins under the stigma; rather prominent sectors between M_4 and Cu_1, at least in the hind wing. In the hind wing, several sectors between M_2 and R_s arise as far proximad as the inner end of the stigma. Northern South America from Colombia to Peru and Brazil. (Fig. 2.)

Polythore[6] Calvert, 1917
(*Thore* Selys, 1853)

5 (4). Venation not so complex, antenodals 20 to 35; cross-veins under the stigma 6 to 10; usually no sectors between M_4 and Cu_1, more than three or four cells long. Between M_2 and R_s no sectors arise proximad of stigma. South America, Venezuela to Peru and Brazil. (Fig. 3.).....**Euthore** Selys, 1869

6 (3). Fore-wing evidently longer and narrower than the hind wing. Main veins appear forked because of the attached sectors. M_2 arising two to four cells beyond the subnodus, especially in the fore-wing. Brazil. (Fig. 4.)

Chalcopteryx Selys, 1853

7 (2). Quadrangle of hind wing scarcely longer than that of the fore wing. Wings petioled about two-thirds of the distance from the base of the wing to the arculus. Fore wing about four and one-half times as long as broad. Arculus often at almost one-half the distance from the wing-base to the subnodus. Mexico to Bolivia. (Fig. 5.).....**Cora** Selys, 1853

8 (1). Cu_2 unbranched, one row of cells between Cu_1, and Cu_2, one row of cells back of Cu_2.....**Miocora** Calvert, 1917

Key to the Genera of the Subfamily Agrioninae

1 (24). Cu_{2a} present. R_s in hind wing usually strongly waved.....2

2 (19). Cu_{2a} running perpendicular to the posterior margin of the wing or toward the base of the wing, and usually with one or more sectors toward the anal angle which are longer than the quadrangle.....3

3 (12). In the hind wing the sectors of that portion of the wing posterior to Cu_2 and distad to Cu_{2a} are generally arched from near the wing margin and not directly attached to Cu_{2a}. True stigma present.....4

[6] Calvert, 1917, proposes the name *Polythore* for this genus, since the name *Thore* is preoccupied.

4 (9). Basal space crossed. Arculus usually distinctly angled and not markedly oblique 5

5 (6). Eight or more cells across the anal area along Cu_{2a}. More than two sectors from Cu_{2a} run toward the anal angle, but they are irregular. Anal margin of hind wing convex. Space between Cu_1 and Cu_2 in hind wing reticulate just beyond MA. China. (Fig. 8.) ..... **Archineura** Kirby, 1894

6 (5). Not more than four to five cells along Cu_{2a} between Cu_2 and the wing-margin. In the fore wing there is one sector from Cu_{2a} toward the anal angle; anal margin not convex. One row of cells between Cu_1 and Cu_2 at their origin 7

7 (8). Nodus less than one-half of the distance from the base of the wing to the stigma. Southern and south-eastern Asia. (Fig. 7.) ..... **Echo** Selys, 1853

8 (7). Nodus more than one-half the distance from the base of the wing to the stigma. Southeastern Asia. (Fig. 6.) ..... **Climacobasis**[7] Laidlaw, 1902

9 (4). Basal space free. Tendency for arculus to be less angled and more oblique 10

10 (11). Cu_{2a} in the hind wing running almost toward the margin, so that it does not reach the length of the quadrangle before sending off a branch toward the anal angle. Western and Central Africa. (Fig. 9.) ..... **Umma** Kirby, 1890 (*Cleis* Selys, 1853)

11 (10). Cu_{2a} in the hind wing running toward the base of the wing, almost the length of the quadrangle before sending a branch toward the anal angle. West Africa. (Fig. 10) ..... **Sapho** Selys, 1853

12 (3). Sectors in that area of the hind wing posterior to Cu_2 and distad to Cu_{2a}, usually (sometimes not in *Agrion*) attached directly to Cu_{2a}. Stigma false or lacking 13

13 (14). Basal space free. Almost cosmopolitan, except for most of Africa and Australia. (Fig. 11.) ..... **Agrion** Fabricius, 1775 (*Calopteryx* Leach, 1815)

14 (13). Basal space crossed 15

15 (16). Broad area in hind wing posterior to Cu_2, with five rows of cells between end of Cu_{2a} and the wing margin which is very convex; in the hind wing the length is less than three and one-half times the breadth. R_s very strongly waved in the hind wing, cutting off a sector anterior to it. All four wings of the male opaque; only one or two cells of the basal space divided. Borneo. (Fig. 12.) **Matronoides** Foerster, 1897

[7] I am not sure that *Climacobasis* is generically distinct from *Echo*. Laidlaw (1903) says of *Climacobasis lugens* and *Echo modesta*, "There can be no doubt that the two species which I founded on a single specimen in each case, are merely male and female of the same species. The generic name may be retained as that of a section of the genus *Echo*, distinguished by the great relative length of the pterostigma in the male, in which it is about three times as long as in the female." Williamson (1904) says, "*Echo* is known to me only from descriptions and figures, but such differences between it and *Climacobasis* appear to exist in the anal region and in the stigmas of the males that, in so far as the two names have been published, their separation seems to me desirable, at least till more critical study can be made."

Since I have had no access to specimens of *Echo*, I shall here follow the precedent made by Williamson. The stigmatic differences in figures six and seven are due to sex rather than genus.

16 (15). Area of hind wing posterior to Cu_2 narrower, with two to four rows of cells between end of Cu_{2a} and wing margin which is not very convex; hind wing about three and one-half times as long as broad. R_s not usually so strongly waved as to cut off an anterior sector.....17

17 (18). M_2 and M_3 not appearing forked. Most cells of basal space divided into two by median nervules. All four wings of male opaque. Cu_{2a} alike in fore and hind wings. Japan and southeastern Asia to India. (Fig. 13.)

Matrona Selys, 1883

18 (17). M_2 and M_3 appearing forked because of attached sectors. Only one or two cells of basal space divided. Front wings of male hyaline. Cu_{2a} in fore wing tends to parallel A. Malaysia. (Fig. 14.).....**Neurobasis** Selys, 1863

19 (2). Cu_{2a} turning away from the wing-base; the sector from Cu_{2a} toward the anal angle shorter than the quadrangle.....20

20 (23). True stigma present. M_{1+2} fusing with R at least in the hind wing. M_{1-3} and M_4 arise separately from arculus. Asian genera.....21

21 (22). Quadrangle approximately as long as the basal space and with four to seven cross-veins; posterior wing-margin near the anal angle not concave. Stigma about three times as long as broad; the distance from the wing-base to the nodus more than two-fifths of the wing length. Posterior end of the medio-anal link more basal than the anterior end. China and Japan. (Fig. 15)

Mnais Selys, 1853

22 (21). Quadrangle one and one-half times as long as the basal space and with ten or more cross-veins; posterior wing-margin near the anal angle very concave. Stigma four times as long as broad; the distance from the wing-base to the nodus less than two-fifths of the wing length. Posterior end of MA not so basal as anterior end. China and Formosa. (Fig. 16.)..**Psolodesmus** McLachlan, 1870

23 (20). Stigma present or not. M_{1+2} not fusing with R. M_{1-3} and M_4 usually arise at a common point, especially in the hind-wing. R_s in the hind wing waved so as to approach M_2 very closely. Africa and Madagascar. (Fig. 17)

Phaon Selys, 1853

24 (1). Cu_{2a} not present. Area posterior to Cu_2 supported by a wide bend of Cu_2. R_s in the hind wing not strongly waved. Quadrangle often very convex anteriorly and widened distally. Arculus not angled, but oblique.....25

25 (26). Basal space free. M_2, M_3, Cu_1, and Cu_2 with attached sectors. Veins and sectors turn sharply toward wing margin. Quadrangle almost as long as the basal space. India to Malaysia. (Fig. 18.).....**Vestalis** Selys, 1853

26 (25). Basal space crossed, distinctly longer than the quadrangle. Sectors intermediate, generally not attaching to the main veins. Veins and sectors not bending sharply toward the wing-margin. R_s and M_3 parallel at the end, with two intervening sectors. Genera of the Western Hemisphere, ranging from Canada to South America. (Figs. 19 and 20.)

Heterina[8] Selys, 1853, and **Lais** Selys, 1853

Key to the Genera of the Subfamily Epallaginae

1 (10). Wings petioled not more than one-half way from the wing base to the arculus. Quadrangle not more than four times as long as broad; with not more than two or three cross-veins. Area posterior to Cu_2, at its widest point, at least one-third the width of the wing at that point with several sectors beyond MA . . . 2

2 (5). Quadrangle with one or two cross-veins; subquadrangle usually with more than two. In the hind wing the basal space generally not more than twice as long as the quadrangle 3

3 (4). Area back of anal vein with only one row of cells to beyond MA, at least in the fore wing. Stigma with anterior proximal angle away from the wing-base. In the fore wing the antenodal cross-veins are less numerous than the postnodal. India to China and Malaysia. (Fig. 21.) . . . . . **Pseudophaea**[9] Kirby, 1890 (*Euphaea* Selys, 1840)

4 (3). Area back of anal vein with two rows of cells to beyond MA. Anterior proximal angle of stigma toward the wing-base. Antenodal cross-veins more numerous than the postnodal. Indo-China to Malaysia. (Fig. 22.) **Dysphaea** Selys, 1853

5 (2). Quadrangle without cross-veins; subquadrangle usually with two or fewer. Basal space generally more than twice as long as the quadrangle 6

6 (7). Basal radial space closed and free. India. (Fig. 23.) **Bayadera** Selys, 1853

7 (6). Basal radial space not closed in both wings 8

[8] The genera *Heterina* and *Lais* now contain so many species with so many intergrading characters, that it is impossible to fix upon any clearly defined characters for the separation of the two genera, without a more detailed study than I have been able to give them. Many species of *Heterina* have several rows of cells back of the anal bridge in the forewings, while *Lais* is supposed to have but two such rows. However, in specimens of *H. donna*, *vulnerata*, *cruentata*, *tricolor*, *titia*, *caja*, *macropus*, etc. some have only two. In many species of *Hetaerina* the males have the base of the wing red. Beyond these characters further ones are unknown to me.

[9] The genus *Paraphaea*, Martin, 1903, would seem, from the description, in the Bulletin of the Museum of Paris 1903, to come in this part of the key, but the description is too incomplete to use for the key. The translation reads as follows: "This new genus is created from a single specimen from Manilla and belonging to the Museum of Paris. It is of the Legion *Euphaea* of M. de Selys. The basal space is free, the median sector (M_3) branches from the principal (M_1) toward the end of the quadrangle; the feet are quite long, the body slender, the fundamental color of the body red, but the ventral surface of the thorax entirely black. The nodus is placed exactly at the middle of the wing. The superior appendages are slightly bent not dilated, the inferior small; the posterior margin of the tenth segment bears a papilla."

Under the specific description of P. *barbata:* "Abdomen 55 mm.; lower wing 41 mm.; 24 antenodals and 24 postnodals to the upper wings; 24 antenodals and 24 postnodals to the lower wings. Wings hyaline, slightly tinged with saffranin, the distal tip of the stigma bordered with brown; the stigma brown, covering seven cells, broad at the middle, narrowed at the two ends which are pointed, especially proximally. Quadrangle small, short, crossed."

8 (9). Basal radial space crossed. M_2 usually arising not more than one cell from sub-nodus. The longest sector between Cu_1 and Cu_2 arising below a point several cells before the level of the subnodus. Greece to Persia. (Fig. 24.)
Epallage Charpentier, 1840

9 (8). Basal radial space free; M_2 tends to arise two cells beyond the subnodus. The longest sector between Cu_1 and Cu_2, especially in the hind-wing, arises almost below the subnodus. In the hind-wing of the male, C has a hump before the arculus. India to Burma. (Fig. 25.).....**Anisopleura** Selys, 1853

10 (1). Wing usually petioled two-thirds or more of the way to the arculus. Length of quadrangle and the number of cross-veins vary. The area posterior to Cu_2 narrow, at its widest point usually less than one-fourth the width of the wing at that point, and with not more than two distinct longitudinal sectors.....11

11 (16). Area posterior to Cu_2 a single row of cells (occasionally two cells wide for a short distance; but if so, Cu_2 is not arched). Quadrangle in the fore wing usually at least six times as long as wide. Beyond MA, M_4 arches forward, Cu_2 backward. M_2 and R_s near the wing-margin generally are parallel and with two rather prominent parallel sectors between.....12

12 (13). Quadrangle generally with two or more cross-veins, at least in one wing. The sector anterior to M_{1a} arising before the inner end of the stigma, at least in the hind wing. India to Malaysia. (Fig. 26.)....**Rhinocypha** Selys, 1853

13 (12). Quadrangle usually with less than two cross-veins. The sector anterior to M_{1a}, if present, not arising before the inner end of the stigma.....14

14 (15). Short sectors between M_1 and M_{1a}. Third antenodal over arculus. Quadrangle uniform in width or widened distally. West Africa to Zanzibar and in Philippines. (Fig. 27.).....**Libellago** Selys, 1853

15 (14). No sectors between M_1 and M_{1a}. Second antenodal over arculus. Quadrangle wider proximally. India to Malaysia. (Fig. 28.)
Micromerus Rambur, 1842

16 (11). Area posterior to Cu_2 with more than one row of cells beyond MA, except in *Dicterias* and *Heliocharis*. (Of these two, *Heliocharis* often has basal space crossed; *Dicterias* has M_2 and R_s ending very near to each other.) M_4 generally not prominently arched beyond MA.....17

17 (34). Quadrangle at least four times as long as wide. Wings generally widest beyond the level of the subnodus.....18

18 (27). Antenodal cross-veins usually more than twelve. Area posterior to Cu_2 of one row of cells only, sometimes two rows in *Neocharis;* or Cu_2 forks and has two rows of cells between the forks. Quadrangle crossed.....19

19 (20). Cu_2 forking; two rows of cells between the forks. First costal antenodal almost over the arculus. Brazil. (Fig. 29.)....**Cyanocharis** Needham, 1903

20 (19). Cu_2 not forking. First costal antenodal generally some distance before the arculus.....21

21 (22). Stigma covering only two to three cells. Supplementary sectors in apex of wing numerous and curved; some attached to the principal veins. Spines on the legs very long. India and China.....**Caliphaea**[10] Selys, 1859

[10] Same as *Notholestes*, McLachlan, 1887. See McLachlan, 1894, Annals and Magazine of Natural History, (6) 13: 435. I have seen neither figures nor specimens of this genus, but descriptions seem to place it in the *Epallaginae*.

22 (21). Stigma covering four to seven cells. Supplementary sectors not attached. Spines on legs medium in length. Genera of South America 23

23 (24). Basal space often crossed. Sectors between M_{1a} and M_2 do not arise before the level of the inner end of the stigma. M_{1+2} forks about two cells beyond the subnodus. Quadrangle with one cross-vein. Brazil. (Fig. 30.)

Heliocharis Selys, 1853

24 (23). Basal space free. M_2 arises within a cell of the subnodus. Quadrangle with one or two cross-veins 25

25 (26). Some sectors between M_{1a} and M_2 arise far before the level of the stigma. Quadrangle with one cross-vein. Brazil. (Fig. 32.) . . . . **Dicterias** Selys, 1853

26 (25). No sectors between M_{1a} and M_2 arise before the level of the stigma. Quadrangle with two cross-veins. British Guiana. (Fig. 31.)

Neocharis Foerster, 1906

27 (18). Antenodal cross-veins usually less than nine. Area posterior to Cu_2 of more than one row of cells, but Cu_2 not symmetrically forked 28

28 (29). Two cross-veins in the quadrangle; two or three often in the subquadrangle. Stigma about three times as long as wide. Fourth antenodal over the arculus. M_2 arising four to five cells beyond the subnodus. Straits Settlements. (Fig. 33.) . . . . **Devadatta** Kirby, 1890

(*Tetraneura* Selys, 1859)

29 (28). No cross-veins in the quadrangle; usually none in the subquadrangle. Stigma about five times as long as wide, fusiform in outline. Second or third antenodal over the arculus 30

30 (33). Genera of the Old World. M_2 not arising more than one cell beyond the subnodus. Sectors present between M_1 and M_{1a}. Second antenodal over the arculus 31

31 (32). M_2 arising at the subnodus, or within one-half cell of it; M_{1a} arising three to five cells beyond M_2. Arculus less than one-half way from the base of the wing to the nodus. Antenodals five to seven. Australia and Malaysia. (Fig. 34.) . . . . **Diphlebia** Selys, 1869

32 (31). M_2 arising one cell beyond the subnodus, M_{1a} five cells beyond M_2. Arculus at one-half the distance from the base of the wing to the nodus. Antenodals generally five. West Africa . . . . **Pentaphlebia**[11] Foerster, 1909

33 (30). A genus of the New World. M_2 arising two to four cells beyond the subnodus. Often no sectors between M_1 and M_{1a}. The third antenodal over the arculus. Colombia. (Fig. 35.) . . . . **Amphipteryx** Selys, 1853

34 (17). Quadrangle about twice as long as wide. Wings widest before the level of the nodus. Antenodals about fifteen. India to China. (Fig. 36.)

Philoganga Selys, 1879

Key to the Disparocyphinae

1. One genus only, characters those of the subfamily. Antenodals ten to twelve in each series. South Celebes. (Fig. 37.) . . . . **Disparocypha** Ris, 1916

[11] Only the description was available for this genus.

Key to the Genera of the Subfamily Lestinae

1 (2). The distal end of the quadrangle cut off almost squarely. The front wing over one-third longer than the hind wing. A short sector present in the fore wing between M_1 and M_{1a}. In the hind wing a sector present between M_4 and Cu_1. The distance between the points of origin of M_3 and the bridge to R_s is almost as long as that from the origin of M_3 to the arculus. Hainan. (Fig. 38.)
Pseudolestes Kirby, 1900

2 (1). The distal end of the quadrangle is not cut off squarely. The fore and hind wings of about the same length. No sector between M_1 and M_{1a} (except in *Ortholestes*). The distance between the origin of M_3 and that of the bridge to R_s is less than the distance from the origin of M_3 to the arculus.....3

3 (4). The quadrangle widened distally and with the superior side over one-half the length of the inferior. No sectors between M_3 and M_4. Two rows of cells between M_4 and Cu_1 at the end of Cu_1, at least in many specimens. West Indies. (Fig. 39.).....**Ortholestes** Calvert, 1891

4 (3). The quadrangle not widened distally and with the superior side scarcely one-half the length of the inferior. One or more sectors between M_3 and M_4, except in *Orolestes*. One row of cells between M_4 and Cu_1.

5 (6). The inner end of the quadrangle in the fore wing almost one-half the length of the lower side. M_{1+2} forking less than two cells beyond the subnodus. The third antenodal space almost twice the length of the first. California to Venezuela. (Fig. 40.).....**Archilestes** Selys, 1862

6 (5). The inner end of the quadrangle one-third or less of the length of the lower side except in *Orolestes*. M_{1+2} forking more than two cells beyond the subnodus, at least in one wing. The third antenodal space not more than one and one-half times the length of the first.....7

7 (8). Wing petioled to within Ac's length of itself. No sectors between M_3 and R_s. The longest sector between M_2 and R_s arises about one-half of the way between the stigma and the origin of M_{1a}. M_{1a} not zigzag. India. (Fig. 41.)
Megalestes Selys, 1862

8 (7). Wing petioled to Ac or nearly so. Sectors present between M_3 and R_s. The longest sector between M_2 and R_s not arising more than three or four cells before the level of the stigma.....9

9 (10). Wings, at least those of the male, with large opaque areas. Cu_2 is the only zigzag vein. Stigma very large, surmounting four to six cells. M_{1+2} forking five to seven cells beyond the subnodus. India....**Orolestes**[12] McLachlan, 1895

10 (9). Wings hyaline. Many of the veins strongly zigzag; i. e. the cells are angled. Stigma shorter, surmounting two to three cells. M_{1+2} forks three to seven cells beyond the subnodus.....11

11 (12). Stigma broad, scarcely two and one-half times as long as wide. R_s zigzag. The anal appendages of the female ovoid, very much depressed, as long as the tenth segment. A single species, from East Indies...**Platylestes**[12] Selys, 1862

[12] Descriptions only have been available for these genera.

12 (11). Stigma narrower, usually three or more times as long as wide 13

13 (14). Wings raised, when at rest. Inner end of quadrangle only one-fifth as long as the inferior side. The prothorax with three scallops posteriorly, the middle one of which is the longest. Europe to Madagascar, New Guinea, and New Caledonia. (Fig. 42.) ..... **Sympycna** Charpentier, 1840

14 (13). Wings held horizontally, when at rest. The prothorax not as above 15

15 (16). The sectors of the arculus arising toward the middle, M_4 about one-half of the way down; hence the quadrangle is narrow with the inner end between one-fourth and one-fifth as wide as the inferior side is long. The quadrangle in the hind wing has a distinctly longer upper side than does that of the fore wing. The upper and lower sides are almost parallel. A genus from Australia and surrounding islands. (Fig. 43.) ..... **Austrolestes** Tillyard, 1913

16 (15). The sectors of the arculus arising nearer its upper end, M_4 about one-third of the way down, hence the inner end of the quadrangle is from one-third to one-fourth of the length of the inferior side. The quadrangle of the front and hind wings essentially alike and triangular in shape because of the narrowing distally. Cosmopolitan, except not in Australia. (Fig. 44.)

Lestes Leach, 1815

Key to the Subfamily Lestoidinae

1. One genus only; the characters those of the subfamily. Australia. (Fig. 45.)

Lestoidea Tillyard, 1913

Key to the Genera of the Subfamily Pseudostigmatinae

1 (6). Secondary sectors numerous; two or more rows of cells between M_{1a} and M_2 for some distance. M_{1+2} forking at more than one-half of the distance from the subnodus to the tip of the wing. Cu_2 short, ending at the level of less than one-half the distance from the fork of M_{1+2} to the tip of the wing. Cu_2 with many forks; several to many cells between Cu_2 and the posterior wing margin 2

2 (5). Quadrangle not crossed; about five times as long as wide. No cross-vein in the subquadrangle. MA before the level of the subnodus. M_{1+2} forking beyond the half-way point between the subnodus and the tip of the wing 3

3 (4). The nodus at one-sixth of the wing length; M_2 arched forward under the stigma so as to make a sharp bend. M_3 forks under the inner end of the stigmatic area, at about fifteen cells from the margin of the wing; Cu_1 forks many cells from the wing-margin. Mexico to Guatemala. (Fig. 46.)

Megaloprepus Rambur, 1842

4 (3). The nodus at one-fifth of the wing length; M_2 not so strongly arched. M_3 forks about five cells from the wing margin or not at all. Cu_1 forks about five cells from the wing margin. Colombia to Brazil and Ecuador. (Fig. 47.)

Microstigma Rambur, 1842

5 (2). The quadrangle with two or three cross-veins, several in the subquadrangle, some of which line up with those in the quadrangle. MA in the hind-wing especially, is at the level of the subnodus. M_{1+2} forking at about half way between the subnodus and the wing tip. Peru and Ecuador. (Fig. 48.)

Anomisma McLachlan, 1877

6 (1). Secondary sectors few; a tendency to only one row of cells between M_{1a} and M_2, if two rows, it is for a short distance only, M_{1+2} forking at less than one-half the distance from the subnodus to the tip of the wing. Cu_2 longer, ending at one-half or more than one-half of the distance from the fork of M_{1+2} to the tip of the wing, at least in the fore wing. Cu_2 unbranched. One or two rows of cells between Cu_2 and the posterior wing margin. One row of cells between R_1 and M_{1+2} before the fork of the latter 7

7 (8). The nodus at one-fifth of the wing length. The hind wing, at least, tends to have two rows of cells between M_{1a} and M_2 for a short distance. M_4 has several short sectors at its end; there are two rows of cells posterior to Cu_2. Mexico to Colombia. (Fig. 49.) . . . . . **Pseudostigma** Selys, 1860

8 (7). The nodus at one-fourth to one-fifth of the wing length. One row of cells between M_{1a} and M_2. No sectors more than a few cells long, except between M_1 and M_{1a}. M_4 usually unbranched. One row of cells between Cu_2 and the posterior wing-margin. West Indies and Mexico to Ecuador. (Fig. 50).

Mecistogaster Rambur, 1842

Key to the Genera of the Subfamily Megapodagrioninae

1 (2). Antenodals three to five, postnodals over fifty; venation very complex, many supplementary sectors from M_1 to the posterior margin of the wing. About ten cross-veins under the stigma. Quadrangle almost rectangular at both ends. Wings not petioled to the level of the arculus. Panama to Costa Rica. (Fig. 51.)

Thaumatoneura McLachlan, 1897

2 (1). Antenodals two to three, postnodals generally not over thirty; venation simpler; supplementary sectors not usually present between M_1 and M_{1a}, and Cu_1 and Cu_2. Cross-veins under stigma six or fewer. Quadrangle generally acute distally. Wings usually petioled beyond the level of the arculus 3

3 (4). R_s arising one cell before the subnodus, M_3 about one-half the distance between the arculus and the subnodus. Supplementary sectors M_{1a} to Cu_2. Wing petioled to the level of one-third to one-half of the distance between the arculus and MA. Formosa. (Fig. 52.) . . . . . **Rhipidolestes** Ris, 1912

4 (3). R_s not arising before the subnodus. M_3 arising nearer the subnodus than the arculus 5

5 (30). R_s arising at or very near the subnodus, M_3 at least one cell before the subnodus 6

6 (7). Area posterior to Cu_2 with four or five rows of cells. Wing petioled to or beyond the level of the arculus. Supplementary sectors from M_{1a} to Cu_1 or Cu_2. Malaysia and Australia. (Fig. 53.) . . . . . **Podopteryx** Selys, 1871

7 (6). Area posterior to Cu_2 with one or two, rarely three rows of cells 8

8 (19). Wing not petioled to the level of the arculus, it may be almost so in *Trineuragrion*, a genus with a third antenodal 9

9 (14). Short sectors present between R_s and M_3 as well as some of the other longitudinal veins 10

10 (11). One or two sectors between M_1 and M_{1a}; others from M_{1a} to M_3 and M_4 and Cu_1. Malaysia. (Fig. 55.) ..... **Rhinagrion** Calvert, 1913 (*Amphilestes* Selys, 1862)

11 (10). No sectors between M_1 and M_{1a} 12

12 (13). Three antenodals, the third one being costal and beyond the arculus. One row of cells back of Cu_2. New Caledonia. (Fig. 54.) .. **Trineuragrion** Ris, 1915

13 (12). Two antenodals. Generally at least two more or less complete rows of cells back of Cu_2. Australian region. (Fig. 56.) ..... **Argiolestes** Selys, 1862

14 (9). No sectors between R_s and M_3 15

15 (16). A genus of the Old World. Three cells below the stigma, postnodals about twenty. Thibet? ..... **Mesopodagrion**[13] McLachlan, 1896

16 (15). Genera of the New World. One cell below the stigma: postnodals about fifteen 17

17 (18). Three rows of cells in the area between M_{1a} and M_2, with two unbroken sectors between M_2 and R_s. In the male the stigma is two and one-half times as long as wide. Brazil. (Fig. 57.) ..... **Megapodagrion** Selys, 1885, sens. strict.

18 (17). Two rows of cells in the area between M_{1a} and M_2 and one sector between M_2 and R_s. Stigma about twice as long as wide. Northern South America. (Fig 58.) ..... **Allopodagrion** Foerster, 1910

19 (8). At least one wing petioled to beyond the level of the arculus 20

20 (21). At least one sector between M_4 and Cu_1. Sectors present M_{1a} to Cu_1. Generally two or more rows of cells back of Cu_2, at least part way. Australian region. (Fig. 56.) ..... **Argiolestes** Selys, 1862, sens. strict.

21 (20). No sectors between M_4 and Cu_1. One row of cells back of Cu_2 22

22 (29). Supplementary sectors between R_s and M_3 as well as M_{1a} to R_s and between M_3 and M_4. Cu_1 not strongly arched beyond MA 23

23 (24). The anterior of the sectors between R_s and M_3 shorter than the posterior one. Five cross-veins under the stigma. The longest sector between M_{1a} and M_2 arising four to six cells before the inner end of the stigma. Between M_3 and M_4 only one sector is more than three or four cells long. Costa Rica to Brazil. (Fig. 59.) ..... **Philogenia** Selys, 1862

24 (23). The anterior of the sectors between R_s and M_3 is longer than the posterior one. Two or three cross-veins under the stigma. The longest sector between M_{1a} and M_2 arises not more than one or two cells before the inner end of the stigma. Between M_3 and M_4 are often two sectors more than three cells long, especially in the hind wing 25

25 (26). Wing not petioled beyond the arculus. At least three cells between MA and the level of the subnodus in the area between M_4 and Cu_1. Supplementary sectors (one or two each) from M_{1a} to M_4. Labuan and Sumatra. (Fig. 60.) **Podolestes** Selys, 1862

26 (25). Wing is petioled beyond the arculus. Two cells between MA and the level of the subnodus in the area between M_4 and Cu_1. Supplementary sectors (two each) from M_{1a} to M_4 27

[13] Description only was available for this genus.

27 (28). Wing petioled to the level of about one-third the length of the quadrangle. Three antenodals. Tendency to a cubito-anal cross-vein before the subquadrangle in addition to the vein Ac. Arculus not beyond the last antenodals. West Africa. (Fig. 62.) ..... **Neurolestes** Selys, 1882

28 (27). Wing petioled to the level of one-half to two-thirds of the length of the quadrangle. Two antenodals. No accessory cross-veins before the subquadrangle. Arculus distinctly beyond the second antenodals. Madagascar. (Fig. 61.)
Nesolestes Selys, 1891

29 (22). No sectors present between R_s and M_3. Cu_1 strongly arched beyond MA. One sector between M_{1a} and M_2 and one between M_2 and R_s. Australia. (Fig. 63.) ..... **Synlestes** Selys, 1869

30 (5). R_s arising at least a cell beyond the subnodus. M_3 usually not before the subnodus, at least not a cell's length before it. The wing petioled to beyond the level of the arculus 31

31 (32). Sectors M_1 to Cu_2. Many sectors between Cu_1 and Cu_2 so that the distance on the hind margin between these two veins is as great as that from the level of MA to the end of Cu_2. Quadrangle very long, almost or quite reaching the subnodus. Wing greatly petioled. Mexico to Central America. (Fig. 64.)
Paraphlebia Hagen, 1861

32 (31). No sectors between M_1 and M_{1a}. Cu_1 and Cu_2 usually ending near together at the wing-margin 33

33 (36). The area behind Cu_2 of two or three rows of cells. Supplementary sectors at least from M_{1a} to Cu_1 34

34 (35). M_3 arising at the subnodus. Ac is slightly beyond the level of the first antenodal. New Guinea. (Fig. 65.) ..... **Wahnesia** Foerster, 1900

35 (34). M_3 arising slightly beyond the subnodus, New Guinea.
Metagrion[14] Calvert, 1913

36 (33). The area posterior to Cu_2 of one row of cells only 37

37 (48). Supplementary sectors rather numerous. Some between R_s and M_3 38

38 (41). Supplementary sectors from M_{1a} to M_4. Old World genera 39

39 (40). M_3 arising from M_{1+2} at the subnodus. Often more than two sectors between M_{1a} and M_2. Quadrangle not reaching the level of the nodus. South Africa. (Fig. 66.) ..... **Chlorolestes** Selys, 1862

40 (39). M_3 arising before the subnodus. Not more than two sectors between M_{1a} and M_2. Quadrangle long, reaching the level of the nodus. Seychelles.
Allolestes[14] Selys, 1869

41 (38). No sectors between M_3 and M_4. Genera of South America 42

42 (43). Antenodals more than two, at least in the hind wings. Ecuador.
Neuragrion[14] Karsch, 1891

43 (42). Antenodals two only 44

44 (47). M_3 separating from M_{1+2} before the subnodus 45

45 (46). Supplementary sectors from M_{1a} to M_3, often none between M_2 and R_s. Usually an accessory cross-vein between Cu and A. Guiana. (Fig. 67.)
Dimeragrion Calvert, 1913

[14] Descriptions only were available for these genera.

46 (45). Supplementary sectors between M_2 and R_s and two long ones between R_s and M_3. No cross-veins in the subquadrangle or before it. Ecuador.
Heteropodagrion[15] Selys, 1885

47 (44). M_3 separating from M_{1+2} beyond the subnodus. Supplementary sectors between M_{1a} and M_2, and R_s and M_3. Colombia ..... **Mesagrion**[15] Selys, 1885

48 (37). No supplementary sectors between R_s and M_3 49

49 (50). R_s arising one cell beyond the subnodus. Two sectors between M_{1a} and M_2, some also between M_2 and R_s, and M_3 and M_4. Cu_1 arched beyond MA. South Africa. (Fig. 66.) ..... **Chlorolestes** Selys, 1862

50 (49). R_s arising at least two or three cells beyond the subnodus. No sectors between M_2 and R_s nor between M_3 and M_4 51

51 (54). At least some supplementary sectors present. Quadrangle not approaching very closely the posterior wing-margin. Cu_1 not strongly arched beyond MA 52

52 (53). One sector between M_{1a} and M_2. Africa and Madagascar.
Protolestes[15] Foerster, 1899

53 (52). Two sectors between M_{1a} and M_2. The New World, from Mexico to Argentina. (Fig. 68.) ..... **Heteragrion** Selys 1862

54 (51). No supplementary sectors except M_{1a}. The quadrangle at its distal end approaches the hind margin of the wing. Cu_1 strongly arched beyond MA 55

55 (56). The fore wing of the male with the inner end of the quadrangle lacking. Ac about one-third of the way from the first to the second antenodals. R_s arising four cells beyond the subnodus in the fore wing, three in the hind wing. The upper side of the quadrangle distinctly shorter than the lower side. Australia. (Fig. 69.) ..... **Chorismagrion** Morton, 1914

56 (55). The quadrangle touching the posterior wing-margin. The wing petioled to M_{1a}. M_3 arising one to one and one-half cells beyond the subnodus. R_s at five to seven cells beyond the subnodus. Costa Rica to Brazil. (Fig. 70.)
Perilestes Selys, 1862

Key to the Genera of the Subfamily Coenagrioninae

1 (22). Quadrangle relatively regular, the upper side two-thirds to three-fourths or more of the length of the lower in both wings. M_4 and Cu_2 scarcely zigzag, so that most of the cells of the wing are four-sided rather than five-sided; the longitudinal veins arranged in a parallel and very regular fashion. Tibial spines and quadrangle relatively long. (Legion *Platycnemis* of Selys for the most part) 2

2 (13). Wings generally plainly not petioled to Ac. R_s arising at the subnodus 3

3 (6). The upper side of the quadrangle more than three-fourths the length of the lower side. Antenodal cells between M_4 and Cu_1 are three to five in number, usually at least four. Ac near the level of the first antenodal cross-veins. The first and second antennal segments short, the third long and slender 4

4 (5). Three to five antenodal cells between M_4 and Cu_1. Arculus under the second antenodals. Africa. (Fig. 71.) ..... **Metacnemis** Selys, 1863

[15] Descriptions only were available for these genera.

5 (4). Four antenodal cells between M_4 and Cu_1. The arculus between the first and second antenodals, much before the second. West Africa.

Mesocnemis[16] Karsch, 1891

6 (3). The upper side of the quadrangle not more than three-fourths the length of the lower side; the antenodal cells three or less between M_4 and Cu_1. Ac generally beyond the level of the first antenodals. Antennae not as above except in *Platycnemis* and *Stenocnemis* 7

7 (10). Cu_2 long, extending beyond the level of the base of M_{1a} which is six to seven cells before the level of the stigma. Postnodals fifteen or more. Posterior tibiae of males not dilated, superior anal appendages at least as long as the inferior 8

8 (9). Three antenodal cells between M_4 and Cu_1. About fifteen postnodal cells in the front wing. The third segment of the antenna shorter than the first plus the second. Cu_2 long, extending beyond the level of the base of M_{1a}, which vein arises six to seven cells before the stigma. India to Burma. (Fig. 72.)

Calicnemis Selys, 1863

9 (8). Two antenodal cells between M_4 and Cu_1. Front wing with eighteen to twenty postnodals. The third segment of the antenna longer than the first plus the second. West Africa ..... **Stenocnemis**[17] Karsch, 1899

10 (7). Cu_2 not extending beyond the level of the base of M_{1a}, the latter arising two to four cells before the stigma. About thirteen postnodals. Two antenodal cells between M_4 and Cu_1. Posterior tibiae of males more or less dilated, superior anal appendages shorter than the inferior 11

11 (12). Cu_2 extending almost to the level of the base of M_{1a}. The second antennal segment as long as the third. Syria to Japan and Sumatra; Madagascar. (Fig. 73.) ..... **Copera** Kirby, 1890

(*Psilocnemis* Selys, 1863)

12 (11). Cu_2 not extending to the level of the base of M_{1a} by several cells. The third antennal segment as long as the first plus the second. Mediterranean Region and China. (Fig. 74.) ..... **Platycnemis** Charpentier, 1840

13 (2). Wings petioled close to or beyond Ac; R_s usually arising beyond the subnodus (sometimes at the subnodus in *Allocnemis*) 14

14 (21). R_s arising within one or two cells of the subnodus 15

15 (20). Wings not petioled to the level of the arculus. Ac almost as near the level of the second antenodal as of the first 16

16 (17). The end of the wing with a denticulate margin. Superior appendages of the male longer than the inferior, which are straight. Malaysia. (Fig. 75.)

Idiocnemis Selys, 1878

17 (16). The end of the wing not denticulate at the margin. Superior appendages not longer than the inferior 18

18 (19). The upper side of the quadrangle not more than three-fourths the length of the lower. Cu_2 extending beyond the subnodus to a distance of thirteen to sixteen cells. Usually six to nine cells between the base of R_s and the point where M_{1+2} forks. India to Malaysia. (Fig. 76.) ..... **Coeliccia** Kirby, 1894

(*Trichocnemis* Selys, 1857)

[16] Description only was available for this genus.

[17] Studied from descriptions only.

19 (18). The upper side of the quadrangle scarcely shorter than the lower. Cu_2 extending six to eight cells beyond the level of the subnodus. Four to five cells between the base of R_s and the forking of M_{1+2}. West Africa to South Africa. (Fig. 77.) ..... **Allocnemis** Selys, 1863

20 (15). Wings petioled beyond the level of the arculus. Ac under or near the level of the first antenodal. R_3 arising one or two cells beyond the subnodus, M_3 at the subnodus. Madagascar. (Fig. 78.) **Tatocnemis** Kirby, 1889
Nesocnemis[18] Selys, 1891

21 (14). R_3 arising four or more cells beyond the subnodus, at least in the front wing. Ac about one-half way between the antenodals. Philippines. (Fig. 79.)
Prionocnemis Kirby, 1890
(*Hypocnemis* Selys, 1863)

22 (1). The quadrangle generally with a very acute distal lower angle, the upper side of the quadrangle usually less than two-thirds the length of the upper side. M_4 and Cu_1 usually zigzag, so that many cells are pentagonal. Wings generally not long nor with the straight appearance of those under rubric (1). (If the wings have the general appearance of those under (1), the quadrangle is acute at the end. If the quadrangle is regular, the postnodals are few in number and the second antenodals are before the arculus.) 23

23 (28). M_4 and Cu_1 not strongly zigzag, so that the principal veins are long, straight and give the wing the straight, uniform appearance of the *Platycnemis* group. Tibial spines relatively long 24

24 (27). In the front wing the inner end of the quadrangle is about as long as the upper side. M_{1+2} forks much nearer the origin of M_{1a} than the subnodus 25

25 (26). The upper side of the quadrangle about one-third as long as the lower side. The superior appendages of the male longer than the inferior, and compressed, and bent at the end. Seychelles. (Fig. 80.) **Leptocnemis** Kirby, 1890
(*Hemicnemis* Selys, 1882)

26 (25). The upper side of the quadrangle about one-half as long as the lower side. The superior appendages of the male thick, short, compressed, and conical in form. Madagascar ..... **Paracnemis**[19] Martin, 1903

27 (24). The inner end of the quadrangle of the fore wing about one-third the length of the upper side; the quadrangle long and narrow. M_{1+2} forking about one-half way between the subnodus and the base of M_{1a}. Chili. (Fig. 81.)
Antiagrion Ris, 1904

28 (23). M_4 and Cu_1 zigzag; M_{1+2} usually curved somewhat at or beyond the subnodal region, instead of running straight out 29

29 (40). Tibial spines long, generally about twice as long as the intervening spaces. In the front wing the inner end of the quadrangle generally longer than the upper part of the arculus and as long as the upper side of the quadrangle. Quadrangle widened distally. Wing not petioled to the level of Ac 30

[18] De Selys' description of *Nesocnemis* fits that of *Tatocnemis* almost exactly; the two are evidently the same genus.

[19] Studied from the description only.

30 (31). Tarsal claws symmetrically cleft, so that the superior and inferior teeth are about equal. The ninth segment of the abdomen almost equals the eighth. The first segment of the antenna scarcely visible; superior male appendages as long as the inferior. Malaysia. . . . . **Onychargia** Selys, 1865

31 (30). Tarsal claws not symmetrically cleft, the superior and inferior teeth not equal. 32

32 (33). The area posterior to Cu_2 tends to be two cells wide and the second antenodal is often slightly beyond the level of the arculus. M_4 becomes zigzag at the level of the fork of M_{1+2}. Mexico to Colombia. (Fig. 82.)

Hyponeura Selys, 1854

33 (32). The area back of Cu_2 of one row of cells only. 34

34 (35). The prolongation of the nodal cross-vein through the vein M_{1+2} is generally at first perpendicular to M_{1+2}. M_{1+2} in the front wing forks six cells beyond the subnodus; in the hind wings four cells beyond. Tibial spines three times as long as the intervening spaces. New Guinea. (Fig. 83.) **Palaiargia** Foerster, 1903

35 (34). The prolongation of the nodal cross-vein through the vein M_{1+2} is not perpendicular to M_{1+2}. 36

36 (37). Cu_2 long, extending to the level of the origin of M_{1a}, especially in the hind wing, and at least ten or twelve cells beyond the subnodus. Generally fourteen or more postnodal cells; three to seven antenodal cells between M_4 and Cu_1. The New World, Moluccas, Cape of Good Hope, Kurile Islands. (Fig. 84.)

Argia Rambur, 1842

37 (36). Cu_2 short, not extending more than four or five cells beyond the level of the subnodus. About ten cells present between the nodus and the stigma. 38

38 (39). An apical spine on segment eight of the female. The arculus slightly beyond the second antenodal. Three antenodal cells between M_4 and Cu_1. West Indies and Central America. (Fig. 86.). . . . . **Argiallagma** Selys, 1876

39 (38). No apical spine on segment eight of the female. The arculus at the second antenodal. Two antenodal cells between M_4 and Cu_1. Brazil. (Fig. 85.)

Diargia Calvert, 1909

40 (29). Tibial spines shorter, scarcely longer than the intervening spaces; if long, the wings are petioled to or beyond Ac. The inner end of the quadrangle usually not longer than the upper part of the arculus in the fore wing, nor longer than the upper side of the quadrangle. Quadrangle generally not widened distally 41

41 (88). No pale post-ocular spots present on a dark background. 42

42 (53). Female with apical spine on segment eight[20]. 43

(A) Wing petioled to the vein Ac. The quadrangle in the front wing with a very pointed distal lower angle, so that the upper side is shorter than or only as long as the inner end. Tenth segment of the abdomen with a deeply cut posterior margin. Considerable blue in the coloration. South America. (Fig. 121.)

Skiallagma Foerster, 1906

[20] The following two genera cannot be fitted into the key, because the females are unknown, but a brief description may aid in their determination.

(B) "Areulus at, or very near to, the second antenodal; M_2 on the hind wings arising nearest the fourth postnodal; costal edge of the stigma of the hing wings shorter than the proximal or distal edges; Cu_1 and Cu_2 not reaching as far distad as the level of origin of M_{1a} and M_2.....; A.....separating from the hind margin proximal to, or less frequently at, the cubito-anal cross-vein....., which is situated nearer the level of the first than of the second antenodal; venation of the tips of front and hind wings similar, abdomen chiefly red, tenth segment of the male not elevated dorsally, vulvar spine?" Considerable orange and red in the coloration, with black markings. Brazil. (Fig. 96.)

Tigriagrion Calvert, 1909

43 (48). Wing not petioled all the way to Ac.....44

44 (47). Genera of the New World.....45

45 (46). Abdomen chiefly red. The costal side of the stigma not shorter than the proximal or distal sides. Cu_1 extending at least to or beyond the level of the base of M_{1a}, Cu_2 to or beyond that of M_2. In the hind wing the inner end of the quadrangle not as long as the upper side. North and South America. (Fig. 88.)

Amphiagrion Selys, 1876

46 (45). Abdomen generally with some red. The costal edge of the stigma is shorter in the hind wing than the proximal or distal sides. Venation otherwise much like the preceding. Mexico and United States. (Fig. 95.)

Hesperagrion Calvert, 1902

47 (44). Genus of the Old World. Front margin of the stigma longer than the posterior one. Quadrangle exceedingly narrow. South Abyssinia.

Thermagrion[21] Foerster, 1906

48 (43). Wing petioled to or beyond Ac.....49

49 (50). A genus of the Old World. Coloration largely black and blue. Tibiae with long spines. Lower tooth of tarsal claw almost as large as the upper. Oceanica. (Fig. 116.).....**Xiphiagrion** Selys, 1876

50 (49). Genera of the New World.....51

51 (52). M_3 not arising very close to the subnodus, but at least one-half cell before it. Coloration light, much red. Color pattern of dorsum of thorax with no markings darker than brown. Some blue often present. South America and Western North America. (Fig. 109.).....**Oxyagrion** Selys, 1876

52 (51). M_3 arising very near the subnodus, not more than one-fifth of a cell before it. Abdomen chiefly reddish and yellowish. (Fig. 127.)

Leptobasis Selys, 1877

54 (42). Female without apical spine on segment eight.....54

54 (55). Two complete rows of cells beyond the stigma between C and R_1, this area much broader than the corresponding one between R_1 and M_1. The wing-margin slightly indented at the stigma. Considerable red in the body coloration. East Indies. (Fig. 87.).....**Oreagrion** Ris, 1913

55 (54). Rarely two complete rows of cells beyond the stigma between C and R_1. Wing-margin not indented at the stigma.....56

[21] Studied from description only.

56 (59). Wing very evidently not petioled to the level of Ac; petiolation ceasing as far before it as Ac is long. 57

57 (58). Colors red and dark bronze. Europe and Mediterranean Region to China. (Fig. 89.) . . . . . **Pyrrhosoma** Charpentier, 1840

58 (57). Coloration without red, but is bronze varied with blue, green, or yellow. Europe, Asia Minor, and Chili? (Fig. 90.) . . . . **Erythromma** Charpentier, 1840

59 (56). Wing petioled very close to the level of Ac 60

60 (71). Genera of the New World 61

61 (68). Wing not petioled beyond Ac. Tarsal claw with rather strong inferior tooth 62

62 (63). Postnodals eighteen to twenty, Cu_2 extending to the level of the base of M_{1a}, which arises four or more cells before the stigma. Colors of the dorsum blue and black; yellow beneath the thorax. United States and Canada. (Fig. 108.)
Chromagrion Needham, 1903

63 (62). Postnodals fourteen or fewer, Cu_2 not extending to the level of the base of M_{1a}, the latter arising one to two cells before the stigma 64

64 (67). Coloration not reddish. Abdomen usually thirty or more millimeters long 65

65 (66). The descending cross-vein from the subnodus continuous to the wing-margin. R_s and M_3 narrowly separated at the proximal cross-vein between them. Tooth on tarsal claw well developed but distinctly shorter than the claw. Male inferior appendages well developed. South America. (Fig. 120.)
Aeolagrion[22] Williamson, 1917

66 (65). The descending cross-vein from the subnodus not continued directly to the wing-margin. Tooth on the tarsal claw large, almost as large as the claw; male inferior appendages rudimentary. R_s and M_3 widely separated at the proximal cross-vein between them. South America. (Fig. 119.)
Leptagrion Selys, 1876, sens. strict.

67 (64). Coloration reddish. Tarsal claw with a small inferior tooth. Abdomen generally less than thirty millimeters long. United States and West Indies to Brazil. (Fig. 122.) . . . . . **Telebasis** Selys, 1865
(*Erythragrion* Selys, 1876)

68 (61). Wing petioled beyond Ac. Tarsal claw with a very small or no inferior tooth 69

69 (70). M_2 arising nearest the fifth or sixth postnodals in the hind wings; at the sixth or beyond in the front wings. Tarsal claw toothless; superior appendages of male not bent down almost at a right angle in their apical half. Genital valves of the female not reaching far beyond the level of the tips of the abdominal appendages. Central America to Brazil. (Fig. 126.)
Metaleptobasis Calvert, 1907

[22] This genus includes *Leptagrion dorsale*, hence *Hylaeagrion* of Foerster, 1906. Williamson (Entom. News, 1917, p. 241) arrives at the conclusion that Foerster's *Hylaeagrion argentolineatum* is in reality *L. dorsale*, and his *H. croceum* Selys is *Leptobasis*, probably *vacillans*. Therefore the generic name *Hylaeagrion* falls, *L. dorsale* becomes the type of *Aeolagrion* and *L. macrurum* is that of *Leptagrion*.

70 (69). M_2 arising nearest the fourth postnodal in the hind wings, the fifth in the front wings. Tarsal claws toothed. The superior appendages of the male bent down almost at a right angle in their apical half. Genital valves of the female reach far beyond the level of the tips of the abdominal appendages. West Indies and Brazil. (Fig. 127.) ..... **Leptobasis** Selys, 1877

71 (60). Genera of the Old World 72

72 (83). M_3 arising very distinctly before the subnodus 73

73 (80). Inferior tooth of tarsal claws well developed, when compared with the superior tooth 74

74 (75). Wing ten to twelve mm. long; areulus distinctly beyond the second antenodal, inner end of quadrangle lacking in the male. Postnodals six to eight. Australia. (Fig. 106.) ..... **Hemiphlebia** Selys, 1860

75 (74). Wing usually twenty or more mm. long; areulus near the level of the second antenodals; inner end of quadrangle present 76

76 (77). Coloration yellowish or reddish. India to Australia and Africa. (Fig. 117.) ..... **Ceriagrion**[23] Selys, 1876

77 (76). Coloration not light 78

78 (79). Largely black. Tibial spines long. Fiji Islands and New Guinea. **Nesobasis**[24] Selys, 1891

79 (78). Bronze and dark. Tibial spines very short. Aru and Bivak Islands. (Fig. 118.) ..... **Papuagrion** Ris, 1913

80 (73). Inferior tooth of the tarsal claw lacking or very small 81

81 (82). Largely black. Tibial spines long. Malaysia and Polynesia. **Nesobasis**[24] Selys, 1891

82 (81). Coloration bronze, varied with green and black, wings broad. Black bands on head, thorax, and abdomen. Africa ..... **Argiagrion**[24] Selys, 1876

83 (72). M_3 arising almost or quite at the subnodus 84

84 (87). R_s arising at the subnodus 85

85 (86). Stigma square or oblong, followed by a single row of cells. Coloration not very metallic. Malaysia. (Fig. 128.) **Teinobasis** Kirby, 1890 (*Telebasis* Selys, 1877)

86 (85). Stigma five-sided and followed by two rows of cells. Malaysia and Polynesia ..... **Pericnemis**[24] Selys, 1863

87 (84). R_s arising beyond the subnodus; M_3 also slightly beyond or at the subnodus. Wing petioled to or beyond the level of the areulus. Malaysia. (Fig. 129.) ..... **Amphicnemis** Selys, 1863

88 (41). Pale postocular spots present on a dark background, although sometimes confluent with the light coloring of the rear of the head; apparently so in those genera with dichromatic females 89

[23] *Ceriagrion* is here used to include *Brachybasis;* in the opinion of Dr. Ris the latter cannot stand as a genus. See p. 317 of his "Odonatanach den Sammlungen L. Schultzes und Katalog der Odonaten von Suedafrika," 1908. Denkschr Med.-natwiss. Ges. Jena, 13: 303-346.

[24] Studied from description only.

89 (94). Stigma in fore and hind wings of males dissimilar in color, size or both Tenth segment of abdomen of male generally with a bifid dorsal process. Female often with apical spine to segment eight of abdomen. Postocular spots, in female at least, tend to disappear. Females dichromatic or polychromatic. . . . 90

90 (91). In the male the stigma of the front wing does not touch the costa. Female with no external black stripe on second or third tibiae. Coloration black, orange, and yellowish. Postocular spots, in females at least, tend to disappear. United States to Venezuela and West Indies. (Fig. 97.)

Anomalagrion Selys, 1857

91 (90). Stigma in male touching C. Female generally with an external black stripe on second and third tibiae 92

92 (93). Penis with pair of erect spines on the penultimate segment. In American species at least, the anterior surface of thorax not solid black. Cosmopolitan. (Fig. 100.) . . . . . **Ischnura** Charpentier, 1840. (*Micronympha* Kirby, 1890)

93 (92). Penis with pair of erect spines on penultimate segment. Anterior surface of thorax solid black, except in green females, middle prothoracic lobe with small tooth on each side. Arizona to Baja California. (Fig. 101.)

Celaenura Kennedy, 1917

94 (89). Stigma in fore and hind wings of male similar 95

95 (102). The second antenodals distinctly before the level of the arculus. Both wings not petioled to Ac, but the vein from Ac back to the wing-margin, that is A′, does not continue the direction of the petioled part of the margin, instead it passes up toward Ac and Ab 96

96 (97). Female with apical spine on segment eight. Postnodals six to seven. Coloration dark bronze, with yellow and blue. Dichromatic females. A genus of the New World—tropical America and the West Indies. (Fig. 102.)

Ceratura Selys, 1876

97 (96). Female without apical spine. Old World genera 98

98 (101). Postnodals five to nine; females dichromatic; very small insects, usually less than 24 mm. long 99

99 (100). Quadrangle of fore wing with upper side less than half as long as the lower side; hence distal angle very acute. Legs very long in comparison with rest of body. Australia. (Fig. 103.) . . . . . **Austrocnemis** Tillyard, 1913

100 (99). Quadrangle of fore wing with upper side one-half or more than one-half of length of lower. Legs short. Australia to India. (Fig. 104.)

Agriocnemis Selys, 1869

101 (98). Postnodals ten to twelve; females not dichromatic; chiefly insects of more moderate size i.e. abdomen of twenty-five or more mm. India to Australia, and in Zanzibar and Madagascar. (Fig. 105.) . . . . **Argiocnemis** Selys, 1877

102 (95). The second antenodals not distinctly before the arculus, or if so, either one wing petioled to Ac or the vein A′ continues direction of the hind margin of wing up to point of petiolation 103

103 (116). Both wings distinctly not petioled to the level of Ac. 104

104 (111). Female without apical spine to segment eight 105

105 (106). Stature very slender, abdomen especially so. Coloration metallic and brilliant, similar in both sexes. Europe, China, North and South America. (Fig. 91.) ..... **Nehalennia** Selys, 1850

106 (105). Stature more robust, abdomen not extremely slender; coloration not very brilliant and dissimilar in sexes 107

107 (108). Postocular spots elongated, almost linear, with other transverse lines between them. Two small clear spots between the ocelli. Superior appendages of male longer than last abdominal segment and arcuate. Europe, Asia Minor, Japan, South Africa. (Fig. 92.) ..... **Cercion**[25] Navas, 1907

108 (107). Postocular spots cuneate or rounded, no spots between the ocelli. Superior appendages often short and straight 109

109 (110). Species of Hawaiian Islands. Characters variable. (Fig. 93.)
Megalagrion[26] McLachlan, 1883

110 (109). Not Hawaiian, nor Australian, otherwise quite cosmopolitan. (Fig. 94.)
Coenagrion Kirby, 1890
(*Agrion* Fabricius, 1775)

111 (104). Female with apical spine on segment eight 112

112 (113). Costal edge of stigma shorter than the proximal or distal edges. Cu_1 reaching the level of base of M_{1a}, Cu_2 that of origin of M_2. Postocular spots sometimes disappearing. United States and Mexico. (Fig. 95.)
Hesperagrion Calvert, 1902

113 (112). Costal edge of stigma as long as proximal or distal edges 114

114 (115). M_2 of hind wing generally arising at or beyond the fourth postnodal, tenth segment of male not elevated. Coloration of male generally blue, of female green or yellow, sometimes blue. Cosmopolitan, not in Australia. (Fig. 98.) ..... **Enallagma** Charpentier, 1840

115 (114). Tenth segment of male elevated and with a bifid dorsal process. Penis with transverse row of short spines at base of distal or spatulate lobe. M_2 of hind wing arises at about the fifth postnodal. California. (Fig. 99.)
Zoniagrion Kennedy, 1917

116 (103). One or both wings petioled practically to or even beyond the level of Ac 117

117 (108). Pale postocular spots widely confluent with the pale color on the rear of the head. M_2 arising nearest the fourth postnodal in the hind wings and the fifth in the front wings. Tarsal claws toothed. Superior appendages of the male bent down almost at a right angle in their apical half. Genital valves of female reaching far beyond the level of the tips of the abdominal appendages. West Indies to Brazil. (Fig. 127.) ..... **Leptobasis**[27] Selys, 1877

[25] *Cercion* has been shown by Kennedy, 1917, Ent. News, to include *C. lindenii*, *C. quadrigerum*, and *C. punctum*, all formerly considered species of *Coenagrion*.

[26] *Megalagrion* was said by Perkins (Fauna Hawaiiensis Vol. I, p. clxxv and Vol. II, pp. 63 to 77 and 693 to 696) to have been separated by McLachlan from the genus *Coenagrion* on inconstant characters. Kennedy (Ent. News, 1917), in a study of the penes of many of the Hawaiian species, considers it probable that all the species of those islands may be considered as comprising the genus *Megalagrion*.

[27] Pale postocular spots not always present. Females sometimes with, sometimes without, vulvar spine. See (52) and (70).

118 (117). Pale postocular spots not widely confluent with the pale color on the rear of the head.....119

119 (124). Female with apical spine to segment eight[28].....120

120 (121). Genus of the New World. Colors bronze and blue or greenish. The eighth or ninth or tenth segments blue. End of tenth more or less prolonged or turned back. Mexico to South America. (Fig. 110.)

Acanthagrion Selys, 1876

121 (120). Genera of the Old World.....122

122 (123). M_3 arising before the subnodus; front wing with twelve to fifteen postnodals. Coloration yellowish, greenish and bluish with black markings. Kilimanjaro and Meru, Africa.....**Mombagrion**[29] Sjöstedt, 1909

123 (122). M_3 arising almost at the subnodus; front wing with nine to twelve postnodals. Coloration black, blue, and dark green. Malaysia and West Africa. (Fig. 123.).....**Aciagrion** Selys, 1892

124 (119). Female without apical spine on segment eight.....125

125 (128). Genera of the New World.....126

126 (127). Tips of the wings similar, abdomen very long and slender. Tenth segment of male not forked. Coloration greenish or yellowish. M_{1a} arising one or two cells before the stigma. Eastern United States and Brazil. (Fig. 111.)

Telagrion Selys, 1876

127 (126). Tips of front and hind wings of male unlike; R_1 and M_1 in the hind wing almost unite at the tip. Segment ten of the male with a tubercle above and two spines. Coloration bluish or reddish, or brownish. Mexico to Central America. (Fig. 125.).....**Anisagrion** Selys, 1876

128 (125). Genera of the Old World.....129

129 (138). M_3 arising quite distinctly before the subnodus. Tarsal claw generally with an inferior tooth.....130

130 (133). Prothorax of female provided with two hooks which project forward..131

131 (132). Ac at or but slightly beyond the level of the first antenodals, not more than one-fourth the distance to the second ones. Coloration blue. Australia. (Fig. 107.).....**Caliagrion** Tillyard, 1912

132 (131). In Australian species, at least, Ac is about one-half way between the first and second antenodals. Superior appendages of male usually forked or hollowed at tips. Africa and Asia to Australia. (Fig. 114.) **Pseudagrion** Selys, 1876

133 (130). Prothorax of female simple, no hooks present.....134

[28] *Skiallagma* sometimes has traces of postocular spots; female unknown. See description in footnote to rubric forty-two.

Myagrion, female unknown. Male described as follows: Color carmine-red. Quadrangle irregular, upper side contained in the lower two and one-half times, in the front wing. Cu_2 thirteen cells long. M_2 arises six cells beyond the subnodus in the front wing, five in the hind wing. Abdomen very slender, legs short, tibial spines weak. Tergum of tenth abdominal segment produced into two spines, but without a tubercle such as occurs in *Anisagrion*. Appendages scarcely as long as these spines. South America, Foerster, 1914.

[29] Studied from description only.

25 (30). M_3 and R_s arising separately and the latter arising at the subnodus 26

26 (27). Legs quite long; femora strongly compressed. Tibial spines long, numerous. Nodus not very oblique, so that Sc ends beyond the level of the base of M_3. Cuba. (Fig. 145.) ..... **Microneura** Selys, 1886

27 (26). Legs short; femora not compressed. Nodus oblique, so that Sc ends before the level of the base of M_3 28

28 (29). Wings narrow, about one-sixth or one-seventh as wide as long. The first antenodal space twice as long as the second and also longer than the third. Ac often very near the level of the first antenodals. Cuba and Central America to Brazil. (Fig. 146.) ..... **Protoneura** Selys, 1857

29 (28). Wings broader, about one-fifth as wide as long. The first antenodal space twice as long as the second, and equal to the third. Ac usually at a level intermediate between the antenodals. British Guiana. (Fig. 147.)

Epipleoneura Williamson, 1915

30 (25). M_3 and R_s joined at their origin into a single vein arising beyond the subnodus; or they may arise as separate veins, but if so, R_s still arises beyond the subnodus 31

31 (32). Cu_1 about two and one-half cells long, so that it passes through the cross-vein coming down from the subnodus. The first and third antenodal costal spaces about equal; the second much shorter, more than one-half of the third. Stigma long and narrow, twice as long as wide. British Guiana. (Fig. 148.)

Epipotoneura Williamson, 1915

32 (31). Cu_1 ending at the cross-vein descending from the subnodus. The three antenodal costal spaces about equal. Wings rather broad, almost one-fourth as wide as long. Stigma shorter 33

33 (34). M_2 in the front wing arises at the seventh postnodal; in the hind wing at the fifth. British Guiana ..... **Phasmoneura**[32] Williamson, 1916

34 (33). M_2 in the front wing arises before the seventh postnodal, usually at or before the sixth; in the hind wing at the fourth or before. British Guiana. (Fig. 149.) ..... **Psaironeura** Williamson, 1915

35 (20). The subquadrangle of about the same length as the space before Ac. Australian genera 36

36 (39). Cu_1 more than one cell long and traversing the cross-vein coming down from the subnodus. The space between the fork of M_{1+2} and the base of M_{1a} is not over two-thirds as great as that between the fork of M_{1+2} and the subnodus 37

37 (38). M_{1a} arising about five cells before the stigma in the hind wing. The quadrangle almost as long as the second antenodal space. Cu_1 extending six to seven cells beyond the quadrangle. New South Wales. (Fig. 139.)

Neosticta Tillyard, 1913

38 (37). M_{1a} arising about three cells before the stigma in the hind wing. The quadrangle shorter than the second antenodal space. Cu_1 extending three to four cells beyond the quadrangle. Australia. (Fig. 140.)

Austrosticta Tillyard, 1908

[32] Description only was available for this genus.

39 (36). Cu_1 not more than one cell long and not reaching the cross-vein which comes down from the subnodus (this true in the hind hind wing at least). The space between the base of M_{1a} and M_{1+2} at least four-fifths of that between the fork of M_{1+2} and the subnodus, in the hind wing.....40

40 (41). Cu_1 less than one cell long. M_3 arising before the subnodus. The stigma longer than wide. The second antenodal space about one-half as long as the third. The space between the forking of M_{1+2} and the base of M_{1a} is longer than that between the subnodus and the forking of M_{1+2}, in the hind wing. Australia. (Fig. 141.).....**Notoneura** Tillyard, 1913

41 (40). Cu_1 about one cell long. M_3 arising beyond the subnodus. The stigma about as wide distally as long. The second antenodal space as long as the third; the space between the base of M_{1a} and the forking of M_{1+2} not as long as that between the subnodus and the forking of M_{1+2} in the hind wing. Australia. (Fig. 142.).....**Oristicta** Tillyard, 1913

42 (19). Ac at or before the level of the first antenodals; Cu_1 usually not extending to the level of the subnodus.....43

43 (50). Cu_1 generally not reduced to a cross-vein, but extending beyond MA. Cu_2 may be lacking. R_1 on lower side of stigma not zigzag, but straight.....44

44 (47). Quadrangle widened distally. Area back of M_4 beyond MA broad, at least one-third as great as the width of the wing at that point.....45

45 (46). Head very small, thorax narrow, legs short, abdomen exceedingly attenuate. About nine postnodals. Australia. (Fig. 141.) **Notoneura** Tillyard, 1913

46 (45). Head larger, thorax not so narrow, but form robust, tibiae with many spines. About fourteen postnodals. Australia. (Fig. 151.)..**Nososticta** Selys, 1860

47 (44). Quadrangle not widened distally. Area beyond MA not so broad as above.....48

48 (49). M_3 in some species arising just beyond subnodus. Cu_1 in species from East Indies is at least two cells long, in Australian species less. In Australian species at least, "both superior and inferior appendages of males somewhat forcipate, the inferior pair prolonged beyond the superior." New Caledonia, Bismarck Archipelago and Torres Straits. (Fig. 150.).....**Isosticta** Selys, 1885

49 (48). M_3 always arising before the subnodus. Cu_1 in the front wing almost always less than two cells long, generally ending in the first cell beyond MA. Malaysia to Bismarck Archipelago. (Fig. 152.).....**Risioneura**[33] gen. nov.

50 (43). Cu_1 reduced to a cross-vein, not extending beyond MA. R_1 on lower side of stigma zigzag. M_3 arising beyond the subnodus. New Guinea. (Fig. 153.) **Selysioneura** Foerster, 1900

[33] This genus is made for those species of *Caconeura* (*Alloneura*) included by Selys (1886) in his second group and differs from *Caconeura*, sens. strict., in having Ac situated under or before the first antenodals and Cu_1 rarely long enough to reach the cross-vein coming down from the subnodus. *R. plagiata* Selys is the genotype; the other species included are *R. insignis* Selys, *R. erythroprocta* Selys, *R. wallacii* Selys, *R. exul* Selys, *R. moluccensis* Selys, *R. flavipennis* Selys, *R. salomonis* Selys, *R. circumscripta* Selys, *R.*

134 (135). Ac at the level of the first antenodals. Postnodals eleven to fifteen. Coloration red. Australia and New Zealand. (Fig. 115.)
Xanthagrion Selys, 1876

135 (134). Ac about half-way between the first and second antenodals. 136

136 (137). Front wing not petioled quite to Ac, the hind wing so petioled. Inferior appendages of male much longer than superiors. New Zealand. (Fig. 112.)
Xanthocnemis Tillyard, 1913

137 (136). Both wings petioled to Ac. Superior appendages of male longer than inferior; small species of blue and bronze color. (Fig. 113.)
Austroagrion Tillyard, 1913

138 (129). M_3 arising very near to subnodus, almost touching base of R_3. Tarsal claw without an inferior tooth. Body slender. Malaysia to Australia. (Fig. 124.) . . . . . **Archibasis** Kirby, 1890
(*Stenobasis* Selys, 1877)

Key to the Genera of the Subfamily Protoneurinae

1 (4). Cu_2 one cell long 2

2 (3). Usually more than 14 postnodal cells. Ac near the level of the first antenodals. M_{1a} arising six to eight cells before the stigma. Cu_1 is six to seven cells long. West Africa. (Fig. 130.) . . . . . **Chlorocnemis** Selys, 1863

3 (2). Less than 10 postnodal cells. Ac about midway between the antenodals. M_{1a} arising one cell before the stigma. Cu_1 is four cells long. Brazil. (Fig. 131.)
Proneura Selys, 1889

4 (1). Cu_2 reduced to a cross-vein or lacking, not projecting beyond MA 5

5 (18). A not reduced to Ac, but extending beyond 6

6 (13). A ending in MA, and not in Cu on the posterior side of the quadrangle, nor in the hind margin of the wing before MA. No "cubito-anal" cross-veins before Ac. That edge of the stigma along the margin of the wing as great as that along R_1. The quadrangle practically uniform in width 7

7 (8). Labium with short lobes. The wings often not petioled to Ac. Cu_1 ending at or beyond the level of the subnodus. India, Africa, Malaysia. (Fig. 132.)
Disparoneura Selys, 1860 sens. strict.

8 (7). Labium with elongate lobes 9

9 (10). Cu_1 ending three to five cells beyond the level of the subnodus. Wing petioled almost to Ac. Front wings with three cells between the subnodus and fork of M_{1+2}. Brazil. (Fig. 134.) . . . . . **Peristicta** Selys, 1860

10 (9). Cu_1 ending within a cell of the level of the subnodus. Wing petioled to or slightly beyond Ac. Often four or more cells between the subnodus and fork of M_{1+2} 11

11 (12). Ac not nearer the level of the second antenodal than of the first. The first antenodal space generally more than one and one-half times as long as the second. Five or more cells in the hind wing beyond the stigma. Tibial spines short. West Indies, Central America to Brazil. (Fig. 133.) . . . . . **Neoneura** Selys, 1860
(*Caenoneura* Kirby, 1890)

12 (11). Ac nearer the level of the second antenodal than of the first. The first antenodal space less than one and one-half times the length of the second. Three or four cells beyond the stigma. Brazil. (Fig. 135.)...**Idioneura** Selys, 1860

13 (6). A ending in Cu under the quadrangle or in the wing margin, but not reaching MA.....14

14 (17). A ending in Cu on the posterior side of the quadrangle. A "cubito-anal" cross-vein generally present before Ac. That edge of the stigma along the wing margin shorter than that along R_1.....15

15 (16). Cu_1 ending generally some distance beyond the level of the fork of M_{1+2}, about two-thirds of the distance from the nodus to the stigma. M_{1+2} forking between one-third and one-half the distance from the subnodus to the stigma. Mexico to Venezuela. (Fig. 136.).....**Palaemnema** Selys, 1860

16 (15). Cu_1 ending not more than a cell or so beyond the fork of M_{1+2}, usually before it, M_{1+2} often forking less than one-third the distance from the subnodus to the stigma. Ceylon to Malaysia. (Fig. 137.).....**Platysticta** Selys, 1860

17 (14). A ending in the hind margin of the wing between Ac and MA. No cubito-anal cross-vein before Ac. The costal edge of the stigma as long as that edge along R_1. Southeastern Asia and Malaysia. (Fig. 138.)

Hypostrophoneura[30] gen. nov.

18 (5). The vein A reduced to Ac, not extending beyond.....19

19 (43). Ac distinctly beyond the level of the first antenodal; Cu_1 usually extending beyond the level of the subnodus.....20

20 (35). The subquadrangle shorter than the portion of the wing behind Cu+A and before Ac. Genera of the New World and two of the East Indies and Southern Asia.....21

21 (24). Genera of the Old World. Labium with short lobes. About sixteen postnodals.....22

22 (23). Accessory cross-vein before Ac. The costal edge of the stigma shorter than that along R_1. India to Malaysia. (Fig. 144.).....**Protosticta** Selys, 1885

23 (22). No accessory cross-vein before Ac. The costal edge of the stigma not shorter than that along R_1. Malaysia. **Disparoneura** Selys, 1860, sens. lat.
Caconeura[31] Kirby, 1890 sens. strict.
Alloneura, Selys, 1860 sens. strict.

24 (21). Genera of the New World. Labium with elongated lobes. About twelve postnodals.....25

[30] This genus is created for those species of *Disparoneura* placed by Selys (1886) in the third group, and has as its type *gomphoides* Rambur. It is distinct from *Disparoneura*, sens. strict., by having A end before MA and not in MA, and by Cu_1 usually being much shorter than in *Disparoneura*. It receives its name from the fact that A turns downward: ὑποστροφη = a turning backward, and νεῦρον = nerve.

[31] As here treated this genus comprises only the first group of *Alloneura* as given by Selys (1886). It, therefore, contains the following species: C. *dorsalis* Selys, C. *lansbergei* Selys, C. *gracillima* Selys, C. *hyperythra* Selys, and C. *dohrni* Krueger. See rubric 49 for *Risioneura*. Dr. Ris and Mr. Laidlaw consider this section of *Caconeura* as belonging to *Disparoneura;* the genus *Caconeura* thus passes out of existence, since *C. dorsalis* is the genotype. See Ris (1915) and Laidlaw (1913).

Kirby, W. F. 1894 (a). Catalogue of the described Neuroptera Odonata (dragonflies) of Ceylon, with descriptions of new species.
Jour. Linn. Soc., 24: 545–566, pls. 41–42.

1894 (b). On a new genus and species of Agrionidae from Foo Chow.
Ann. Mag. Nat. Hist., (6) 13: 84–86.

1894 (c). Note on *Archineura basilactea* Kirby.
Ann. Mag. Nat. Hist., (6) 13: 450–451.

1900. On a small collection of Odonata (dragonflies) from Hainan collected by the late John Whitehead.
Ann. Mag. Nat. Hist., (7) 5: 530–539, pl. 12.

Laidlaw, F. F. 1902. On a collection of dragonflies made by members of the Skeat expedition in the Malay peninsula in 1899–1900.
Proc. Zool. Soc. London: 63–92, 381–389, pls. 5–6.

1913. Contributions to a study of the dragonfly fauna of Borneo. Part I.
Proc. Zool. Soc. London: 63–80, pl. 4.

1915. Notes on Oriental dragonflies in the Indian Museum, No. 3. Indian species of the "legion" Protoneura.
Rec. Ind. Mus. Calcutta, 11: 387–391.

1916. Notes on Oriental dragonflies in the Indian Museum, No. 4. The genus *Pseudagrion*.
Rec. Ind. Mus. Calcutta, 12: 21–25.

Martin, R. 1903. Odonates indo-oceaniens des collections du muséum.
Bull. Mus. Paris, 8: 506–512.

McLachlan, R. 1870. Description of a new genus and four new species of Calopterygidae, and of a new genus and species of Gomphidae.
Trans. Ent. Soc. London, 165–170.

1895. Some new species of Odonata of the legion Lestes, with notes.
Ann. Mag. Nat. Hist., (6) 16: 19–28.

1896. On Odonata from the province of Szechuen, in western China, and from Moupin in Eastern Thibet.
Ann. Mag. Nat. Hist., (6) 17: 364–374.

1897. *Thaumatoneura inopinata*, a new genus and species of Calopteryginae.
Entom. Mo. Mag., (2) 8: 130–131.

Morton, K. J. 1914. A remarkable new genus and species of Odonata, of the legion Podagrion Selys, from North Queensland.
Trans. Entom. Soc. London: 169–172, pl. 9.

Muttkowski, R. A. 1910 (a). The applicability of certain generic names of Odonata. 1. *Agrion* versus *Calopteryx*.
Bull. Wis. Nat. Soc., Milwaukee, 8: 158–160.

1910 (b). Catalogue of the Odonata of North America.
Bull. Public Museum City of Milwaukee, 1: 1–207.

Navas, L. 1907. Neuropteros de Espana y Portugal.
Broteria, S. Fiel, 6: 43–100.

Needham, J. G. 1903 (a). A genealogic study of dragonfly wing venation.
Proc. U. S. Nat. Mus., 26: 703–764, pls. 31–54.

1903 (b). A new genus and species of dragonfly from Brazil.
Proc. Ent. Soc. Washington, 16: 55–58.

1903 (c). Aquatic insects in New York State. Part 3, Life histories of Odonata, suborder Zygoptera.
Bull. New York Mus., 68: 218–279, pls. 11–19.

1917. Notes on some recent studies of dragonfly wing tracheation. (Odon.)
Entom. News, 28: 169–173.

Perkins, R. C. L. 1899. Neuroptera. (in)
Fauna Hawaiiensis, 2: 31–89, pls. 3–5.

Rambur, J. P. 1842. Histoire naturelle des insectes Neuropteres.
Paris.

Ris, F. 1898. Neue Libellen vom Bismarck-Archipel.
Entom. Nachrichten, 24: 321–327.

1900. Libellen vom Bismarck-Archipel gesammelt durch Prof. Friedr. Dahl.
Arch. Naturg., 66: 175–204, pls. 9–10.

1904. Odonaten.
Hamburg. Magalhaen. Reise, 7: 44 pp.

1911. Libellen von Sintang, Borneo gesammelt von Dr. L. Martin.
Ann. Soc. Entom. Belgique, 55: 231–255.

1912. Neue Libellen von Formosa, Südchina, Tonking, und den Philippinen.
Suppl. Entom., Berlin, 1: 44–85, 3 pls.

1913 (a). Die Odonaten von Dr. H. A. Lorentz's Expedition nach Südwest New-Guinea 1909 und einige Odonaten von Waigeu. Nova Guinea. Resultats de l'expedition scientifique néerlandaise à la Nouvelle Guinee, 9 Leiden: 471–512.

1913 (b). Odonata von den Aru- und Kei- Inseln gesammelt durch Dr. H. Merton 1908, nebst Übersicht über die von den Aru-Inseln bekannten Odonaten.
Abh. Senckenb. Ges. Frankfurt a. Main, 34: 501–536, 1 pl.

1915. Libellen (Odonata) von Neu-Caledonien und den Loyalty-Inseln.
F. Sarasin und J. Roux, Nova Caledonia, Zoologie, 2: 57–72, 11 fig.

1916 (a). Über Ontogenese der Flügeladerung bei den Libellen.
Mitth. Schweiz. Entom. Ges., 28: pp.

1916 (b). Zwei Notizen über Calopterygiden (Odonata) vom Malaiischen Archipel.
Entom. Mitth., Berlin, 5: 303–318, 9 figs.

Schmidt, E. 1915. Vergleichende Morphologie des zweiten und dritten Abdominalsegments bei männlichen Libellen.
Zool. Jahrb., 39: 87–196, pls. 9–11, figs. A–Z.

VI—A PARTIAL LIST OF THE MOST IMPORTANT REFERENCES CONSULTED IN THE PREPARATION OF THIS PAPER

Calvert, P. P. 1891. A new genus and species of Odonata from Jamaica.
Entom. News, 2: 199.

1893 (a). Catalogue of the Odonata (dragonflies) of the vicinity of Philadelphia, with an introduction to the study of this group of insects.
Trans. Amer. Entom. Soc., 20: 152–172, pls. 2–3.

1893 (b). The Odonate genus *Ortholestes*.
Proc. Acad. Nat. Sci. Philadelphia, 45: 377–382, fig.

1898. Odonata. A synonym and the bearing of its discovery on the classification of *Agrion*.
Entom. News, 9: 72.

1901–1908. Odonata. (in)
Biologia Centrali-Americana, Neuroptera: 17–420, 10 pls.
London, R. H. Porter and Dulau and Co.

1902. On the systematic position of *Thaumatoneura inopinata* McLachlan (Order Odonata), with some remarks on the classification of the suborder Zygoptera.
Entom. Mo. Mag., 38: 29–32.

1904. *Thaumatoneura* again.
Entom. News, 15: 216.

1909. Contributions to a knowledge of the Odonata of the Neotropical region, exclusive of Mexico and Central America.
Ann. Carnegie Mus., 6: 73–280, pls. 1–9.

1913. The fossil Odonate *Phenacolestes*, with a discussion of the venation of the legion Podagrion Selys.
Proc. Acad. Nat. Sci. Philadelphia, 65: 225–272, pl. 14.

Calvert, P. P. 1917. Studies in Costa Rican Odonata, 8. A new genus allied to *Cora*.
Entom. News, 28: 259–263, figs.

Campion, H. 1913. The antenodal reticulation of the wings of Agrionine dragonflies.
Proc. Acad. Nat. Sci. Philadelphia, 65: 220–224.

Comstock, J. H. and Needham, J. G. 1898. The wings of insects. Chap. 4, III. The venation of the wings of the Odonata.
Amer. Natural., 32: 903–911.

selysi Foerster, *R. finisterrae* Foerster, *R. eburnea* Foerster, *R. fruhstorferi* Krueger, *R. pseudexul* Ris, *R. nigrifrons* Ris, *R. marina* Ris, *R. rosea* Ris, *R. dorsonigra* Martin, and *R. torrenticola* Foerster. It is dedicated to Dr. Ris, who has given us the most careful recent treatment of this group. See F. Ris, 1913, Odonata von den Aru-und Kei-Inseln, pages 508 to 514.

Foerster, F. 1897 (a) Beiträge zur kenntniss der indo-australischen Odonatenfauna, IV.
Wien Entom. Zeitung, 16: 101–103.
1897 (b) Beiträge zur kenntniss der indo-australischen Odonatenfauna, VI.
Entom. Nachrichten, 23: 333–338.
1899. Zur Odonatenfauna von Madagascar.
Entom. Nachrichten, 25: 186–191.
1900. Odonaten aus Neu-Guinea.
Termes. Fuzetek, 23: 81–108, figs.
1903. Odonaten aus Neu-Guinea III.
Ann. Mus. Hungar., 1: 509–554.
1906 (a). Neotropische Libellen.
Insektenbörse, 23: 15–16.
1906 (b). Libellen. (Forschungsreise durch Südschoa, Galla und die Somaliländer v. C. Frhr. v. Erlanger.)
Jahrb. Ver. Naturk. Wiesbaden, 59: 299–344, 1 pl.
1909. Beiträge zu den Gattungen und Arten der Libellen.
Jahrb. Ver. Natk. Wiesbaden, 62: 211–235.
1910. Beiträge zu den Gattungen und Arten der Libellen.
Entom. Zeitung, Wien, 29: 51–56.
Hagen, H. 1861. Synopsis of the Neuroptera of North America.
Smithsonian Mis. Coll., 345 pp.
Handlirsch, A. 1906–1908. Die fossilen Insecten und die Phylogenie der rezenten Formen. Ein Handbuch fuer Palaeontologen und Zoologen. 2 vols., 51 pls.
Leipzig, Verlag von Wilhelm Engelmann.
Karsch, F. 1891 (a). Neue Odonaten von Ecuador.
Societas Entom., 6: 105–121.
1891 (b). Übersicht der von Herrn Dr. Paul Preuss in Deutsch-West-Afrika 1890 gesammelten Odonaten.
Entom. Nachrichten, 17: 65–80.
1895. *Archineura basilactea* W. F. Kirby = *Echo incarnata* Karsch.
Entom. Nachrichten, 20: 84.
1899. Odonaten von Johann-Albrecht-Höhe (Nord-Kamerun), gesammelt von Herrn Leopold Conradt.
Entom. Nachrichten, 25, 161–176.
Kennedy, C. H. 1917. Notes on the life-history and ecology of the dragonflies (Odonata) of central California and Nevada.
Proc. U. S. Nat. Mus., 52: 483–635, 404 figs.
Kirby, W. F. 1889. Descriptions of new genera and species of Odonata in the collection of the British Museum, chiefly from Africa.
Proc. Zool. Soc. London, 299–303.
1890. A synonymic catalogue of Neuroptera Odonata, or dragonflies, with an appendix of fossil species.
Gurney and Jackson, London.

Plate IV

Fig. 16.—Front wing of *Psolodesmus dorothea* Williamson. (Male, after Williamson.)
Fig. 17.—Front wing of *Phaon iridipennis* Burmeister. (Male, Cornell Collection.)
Fig. 18.—Front wing of *Vestalis gracilis* Rambur. (Female, Cornell Collection.)
Fig. 19.—Front wing of *Hetaerina americana* Fabricius. (Female, Cornell Collection.)
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Fig. 26.—Front wing of *Rhinocypha biforata* Selys. (Male, after Williamson.)
Fig. 27.—Front wing of *Libellago caligata* Selys. (Female, Cornell Collection.)
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Fig. 65.—Front wing of *Walnesia montivagans* Foerster. (Male, in Acad. Nat. Sci. Philadelphia.)
Fig. 66.—Hind wing of *Chlorolestes fasciata* Burmeister. (Female, in British Museum. From photograph by F. W. Campion.)

Selys-Longchamps, E. de. 1853. Synopsis des Caloptérygines.
Bull. Acad. Belg., (2) 1: 73 pp.
1854. Monographie des Caloptérygines avec collaboration H. Hagen.
Mem. Soc. R. Science de Liége, 9.
1857. Neuroptères de l'isle de Cuba.
De la Sagra Hist. Cuba, 7: 183–201.
1859. Additions au synopsis des Caloptérygines.
Bull. Acad. Belg., (2) 7: 437–451.
1860. Synopsis des Agrionines. Première légion: Pseudostigma.
Bull. Acad. Belg., (2) 10: no. 6.
1860. Dernière légion: Protoneura.
L. c., (2) 10: 431–462.
1862. Seconde légion: Lestes.
L. c., (2) 13: 288–338.
1862. Troisiéme légion: Podagrion.
L. c., (2) 13 : 5–44.
1863. Quatrième légion: Platycnemis.
L. c., (2) 16: 147–176.
1865. Cinquième légion: Agrion.
Genre *Argia*, l. c. (2) 20: 375–414.
1875. Genre *Agrion*, l. c., (2) 41: 247–322, 496–539, 1233–1309.
(2) 42: 490–531, 953–999.
1877. Genres *Telebasis*, *Argiocnemis*, et *Hemiphlebia*.
L. c., (2) 43: 97–159.
1882. Odonates des Phillippines.
Anal. de la Soc. Esp. de Hist. Nat., 11: 1–5, 19–31.
1883. Les Odonates du Japon.
Ann. Soc. Entom. Belg. 27: 82–87, 128–138.
1886. Revision du synopsis des Agrionines.
Mem. Cour. Acad. Belg., 28: 1–233.
1889. *Palaeophlebia*.
Ann. Soc. Entom. Belg., 33.
1891. Causeries odonatologiques, no. 5.
Compt. Rendu. Soc. Entom. Belgique, 35: cccxcviii–cccciii.

Sjöstedt, Y. 1909. Pseudoneuroptera. 1. Odonata.
Sjöstedt's Kilimandjaro-Meru Expedition, 14: 1–52, pls. 1–2. Stockholm.

Tillyard, R. J. 1911. On the genus *Diphlebia* with descriptions of new species and life-histories.
Proc. Linn. Soc. New So. Wales, 36: 584–604, pls. 19–20.
1912. On some new and rare Australian Agrionidae, (Odonata).
L. c., 37: 404–479.
1913. Some descriptions of new forms of Australian Odonata.
L. c., 38: 229–241, pl. 15.
1914. On some problems concerning the development of the wing venation of the Odonata.
L. c., 39: 163–216, pls. 11–13.

Tillyard, R. J. 1915. On the development of the wing venation in Zygopterous dragonflies, with special reference to the Calopterygidae.
L. c., 40: 212–230, figs.
1916. Further researches upon the problems of the radial and zygopterid sectors in the wings of Odonata, and upon the formation of bridges.
L. c., 41: 871–887, 6 figs.
Williamson, E. B. 1901. The dragonflies of Indiana.
Report Dept. Geol. Indiana, 24: 229–333.
1904 (a). The dragonflies (Odonata) of Burma and Siam. I. Subfamily Calopteryginae.
Proc. U. S. Nat. Mus., 28: 165–187, figs.
1904 (b). A new species of *Psolodesmus* (order Odonata) from Formosa.
Entom. News, 15: 247–250, 1 pl.
1913. The medio-anal link in the Agrioninae.
L. c., 24: 258–261.
1915. Notes on neotropical dragonflies or Odonata.
Proc. U. S. Nat. Mus., 48: 601–638, pls. 36–40.
1916. A new dragonfly genus of the legion Protoneura, (Odonata).
Entom. News, 27: 30–33, figs.
1917. Some species of *Leptagrion* with descriptions of a new genus and a new species (Odonata).
L. c., 28: 241–255, pls. and figs.

Explanation of Plates

Plate I

Fig. 1.—Wings of *Epiophlebia superstes* Selys. (Female, Cornell Collection.)
Fig. 2.—Hind wing of *Polythore gigantea* Selys. (Male, Cornell Collection.)
Fig. 3.—Hind wing of *Euthore fasciata* Selys. (Female, Cornell Collection.)
Fig. 4.—Hind wing of *Chalcopteryx rutilans* Rambur. (Male, Cornell Collection.)

Plate II

Fig. 5.—Hind wing of *Cora marina* Selys. (Male, Cornell Collection.)
Fig. 6.—Hind wing of *Climacobasis modesta* Laidlaw. (Male, after Williamson.)
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Fig. 10.—Hind wing of *Sapho ciliata* Fabricius. (Female, Acad. Nat. Sci. Philadelphia.)

Plate III

Fig. 11.—Hind wing of *Agrion virgo* Linnaeus. (Female, Cornell Collection.)
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Plate XIX

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Fig. 139.—Hind wing of *Neosticta canescens* Tillyard. (Male, after Tillyard.)
Fig. 140.—Hind wing of *Austrosticta fieldi* Tillyard. (Male, after Tillyard.)
Fig. 141.—Hind wing of *Notoneura solitaria* Tillyard. (Male, after Tillyard.)
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Fig. 144.—Hind wing of *Protosticta* sp.? (Female, in British Museum. From photograph by F. W. Campion.)

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Fig. 149.—Hind wing of *Psaironeura remissa* Williamson. (Male, after Williamson.)

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Fig. 73.—Hind wing of *Copera marginipes* Rambur. (Male, in Acad. Nat. Sci. Philadelphia.)
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Fig. 78.—Hind wing of *Tatocnemis malgassica* Kirby. (Cornell Collection. From photograph by J. G. Needham.)
Fig. 79.—Front wing of *Prionocnemis haematopus* Selys. (After Selys.)
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Fig. 87.—Front wing of *Oreagrion lorentzi* Ris. (After Ris.)
Fig. 88.—Front wing of *Amphiagrion saucium* Burmeister. (Female, Cornell Collection. From photograph by J. G. Needham.)
Fig. 89.—Front wing of *Pyrrhosoma nymphula* Sulzer. (Male, Cornell Collection.)
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Fig. 94.—Hind wing of *Coenagrion puella* Linnaeus. (Female, Cornell Collection.)
Fig. 95.—Hind wing of *Hesperagrion heterodoxum* Selys. (From photograph by J. G. Needham.)
Fig. 96.—Hind wing of *Tigriagrion aurantinigrum* Calvert. (After Calvert.)
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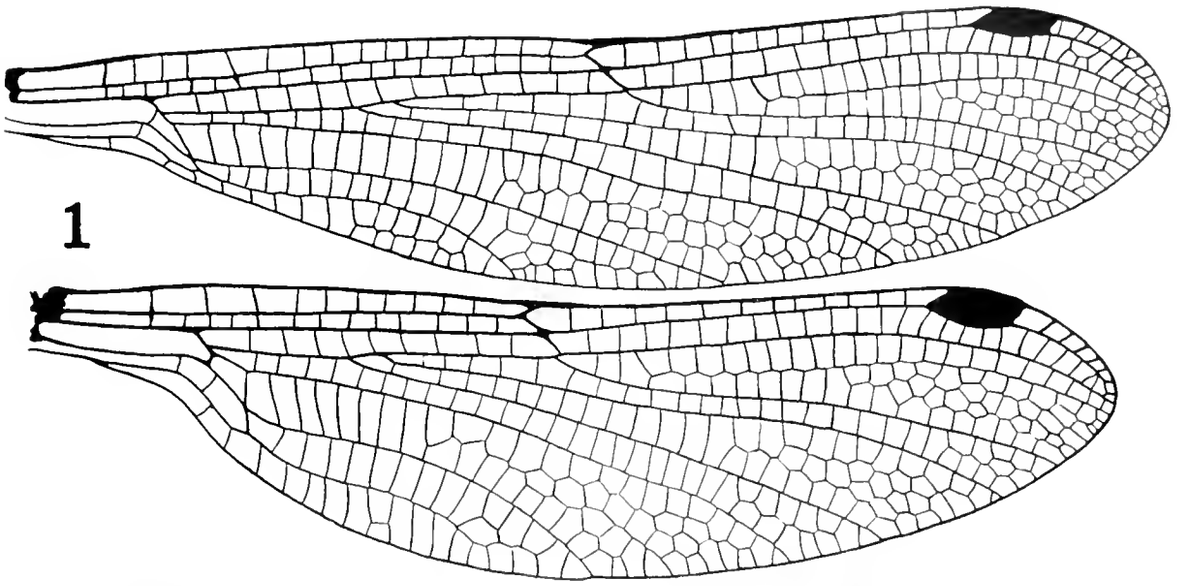
Fig. 102.—Hind wing of *Ceratura capreola* Hagen. (Cornell Collection. From photograph by J. G. Needham.)
Fig. 103.—Hind wing of *Austrocnemis splendida* Martin. (Male, in collection of Carnegie Museum. From drawing by C. H. Kennedy.)
Fig. 104.—Front wing of *Argiocnemis pulverulans* Selys. (After Needham.)
Fig. 105.—Front wing of *Argiocnemis rubescens* Selys. (Female, in Carnegie Museum. From drawing by C. H. Kennedy.)
Fig. 106.—Front wing of *Hemiphlebia mirabilis* Selys. (Male, Cornell Collection.)
Fig. 107.—Part of hind wing of *Caliagrion billinghursti* Martin. (Male, after Tillyard.)
Fig. 108.—Hind wing of *Chromagrion conditum* Selys. (After Needham.)

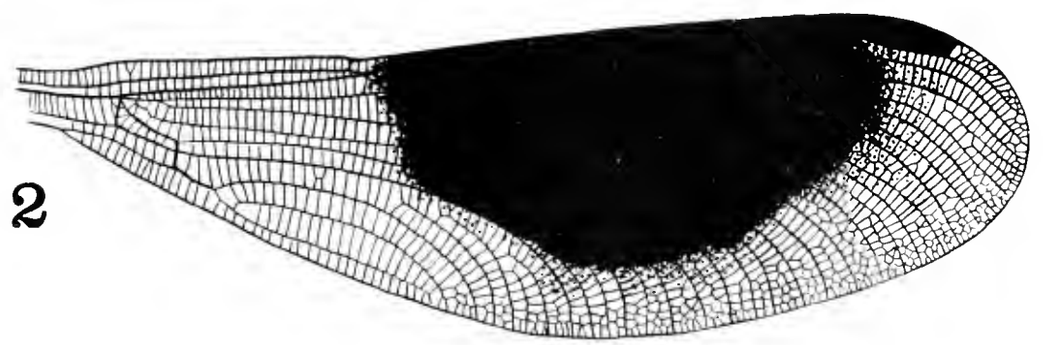
Plate XVI

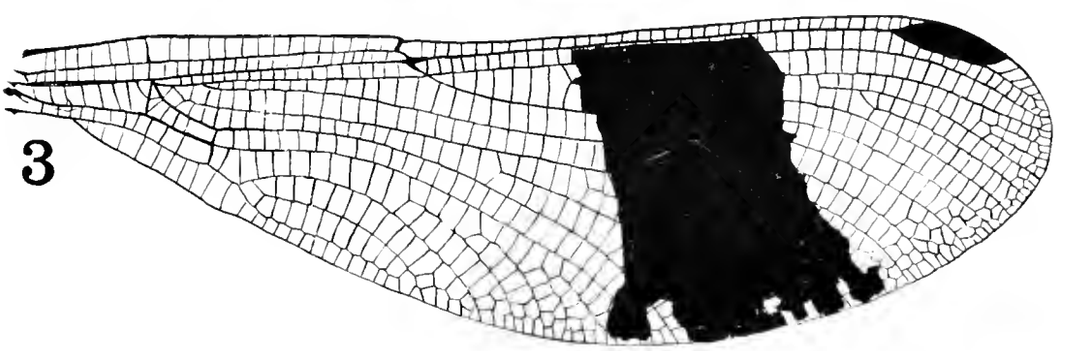
Fig. 109.—Front wing of *Oxyagrion rufulum* Hagen. (Male, Cornell Collection.)
Fig. 110.—Front wing of *Acanthagrion gracile* Rambur. (From photograph by J. G. Needham.)
Fig. 111.—Front wing of *Telagrion longum* Selys. (After Calvert.)
Fig. 112.—Front wing of *Xanthocnemis zelandicum* McLachlan. (Female, Cornell Collection.)
Fig. 113.—Part of hind wing of *Austroagrion cyane* Selys. (Male, after Tillyard.)
Fig. 114.—Front wing of *Pseudagrion furcigerum* Rambur. (Male, from photograph by J. G. Needham.)
Fig. 115.—Front wing of *Xanthagrion erythroneurum* Selys. (From photograph by J. G. Needham.)
Fig. 116.—Front wing of *Xiphiagrion cyanomelas* Selys. (Male, after Ris.)

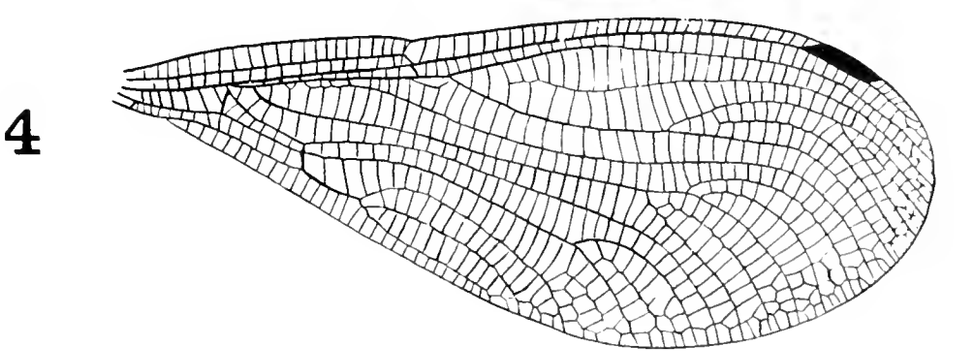
Plate XVII

Fig. 117.—Hind wing of *Ceriagrion coromandelianum* Fabricius. (Male, after Needham.)
Fig. 118.—Hind wing of *Papuagrion occipitale* Selys. (After Ris.)









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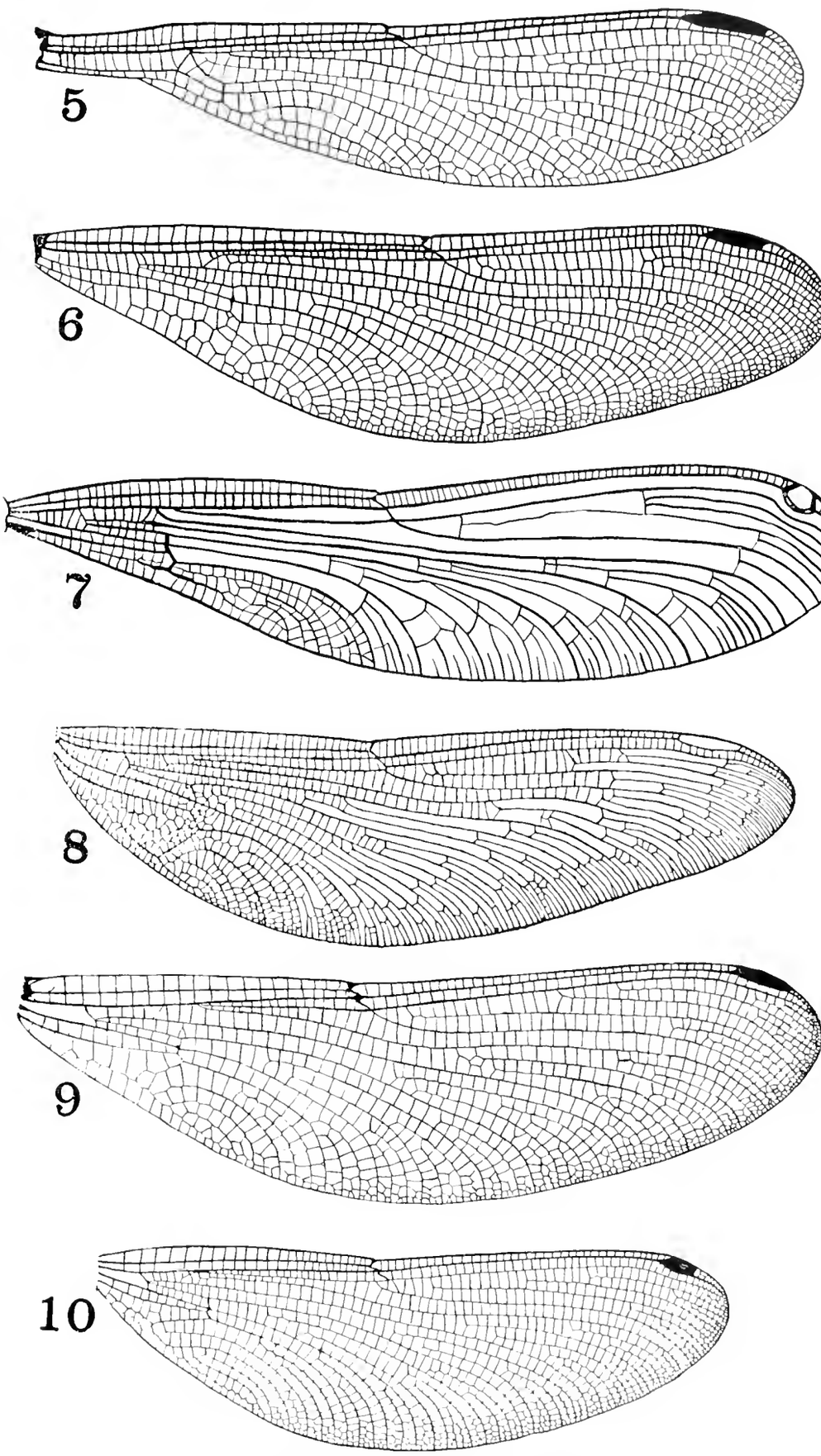

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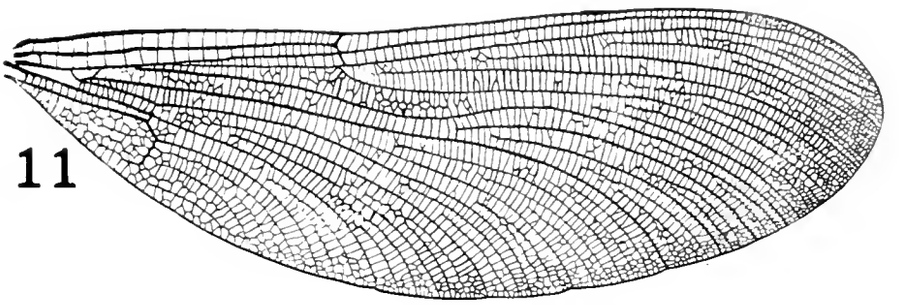

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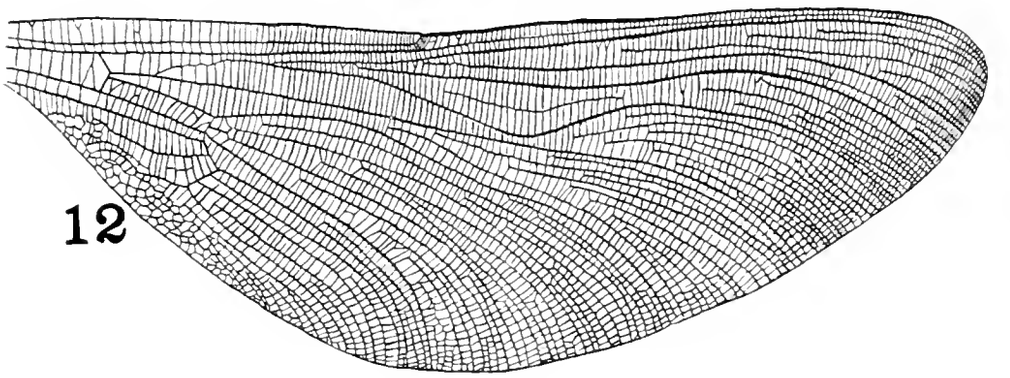

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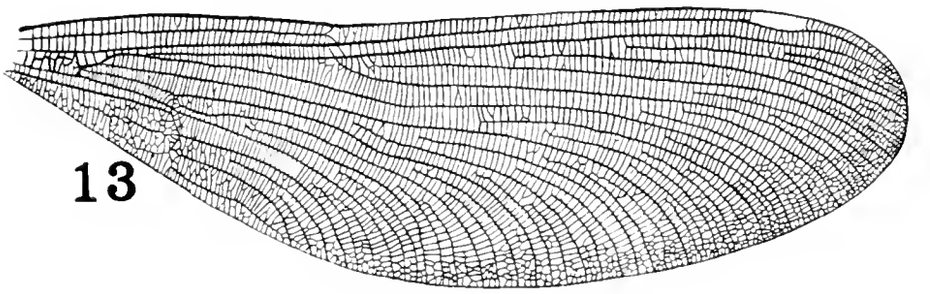

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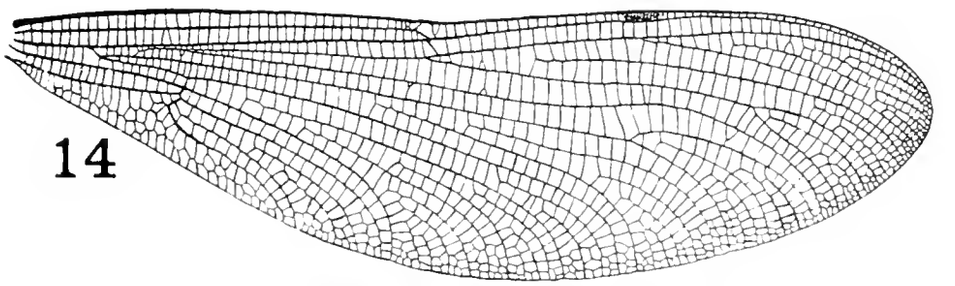

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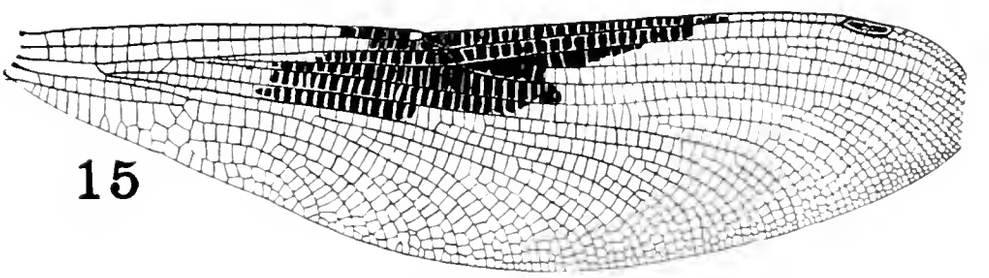

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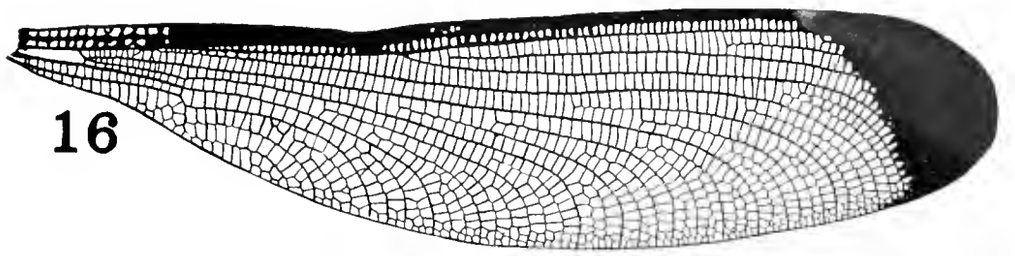

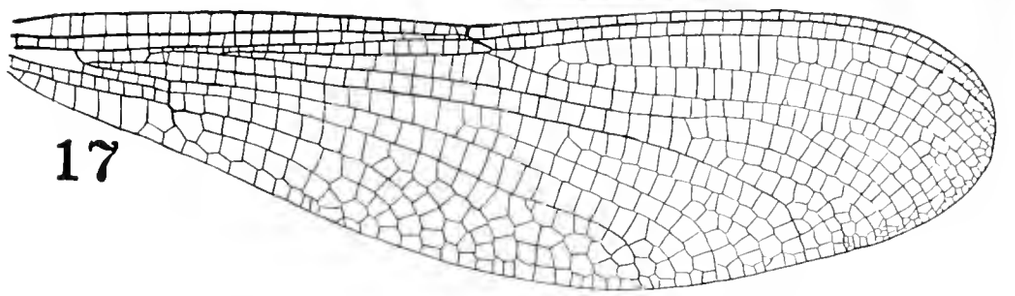

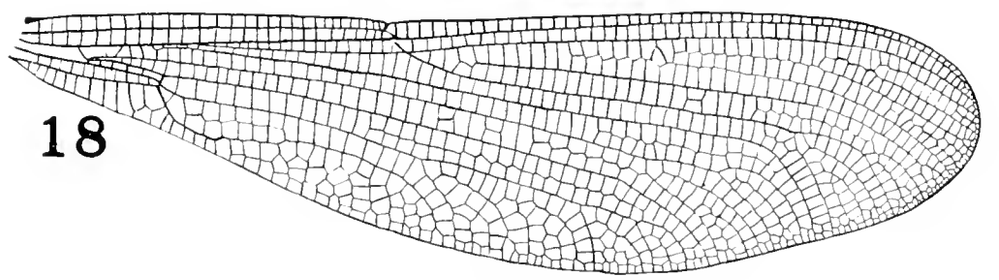

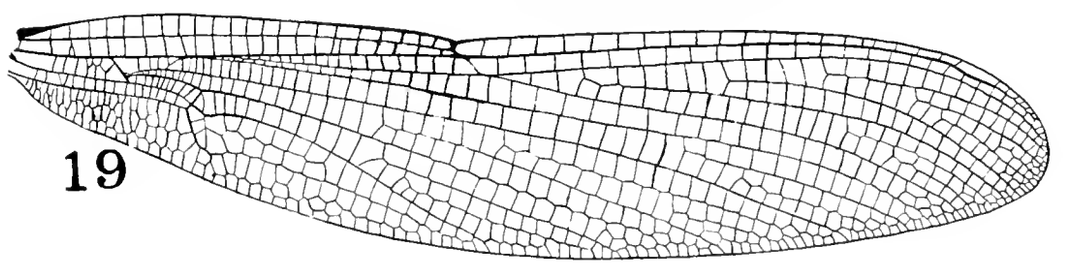

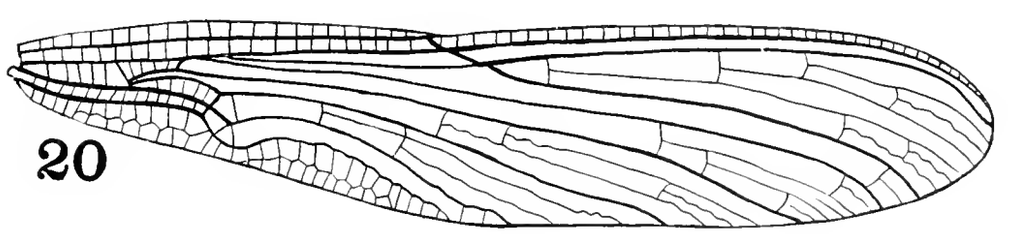

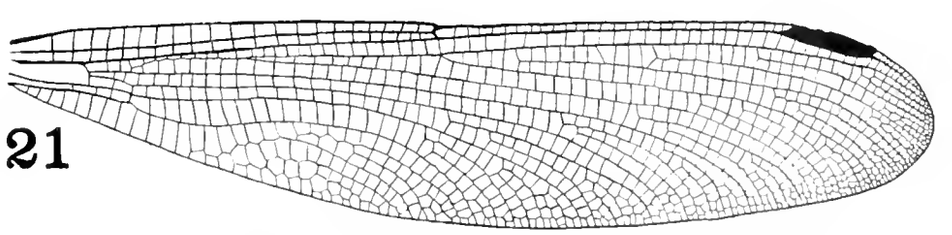

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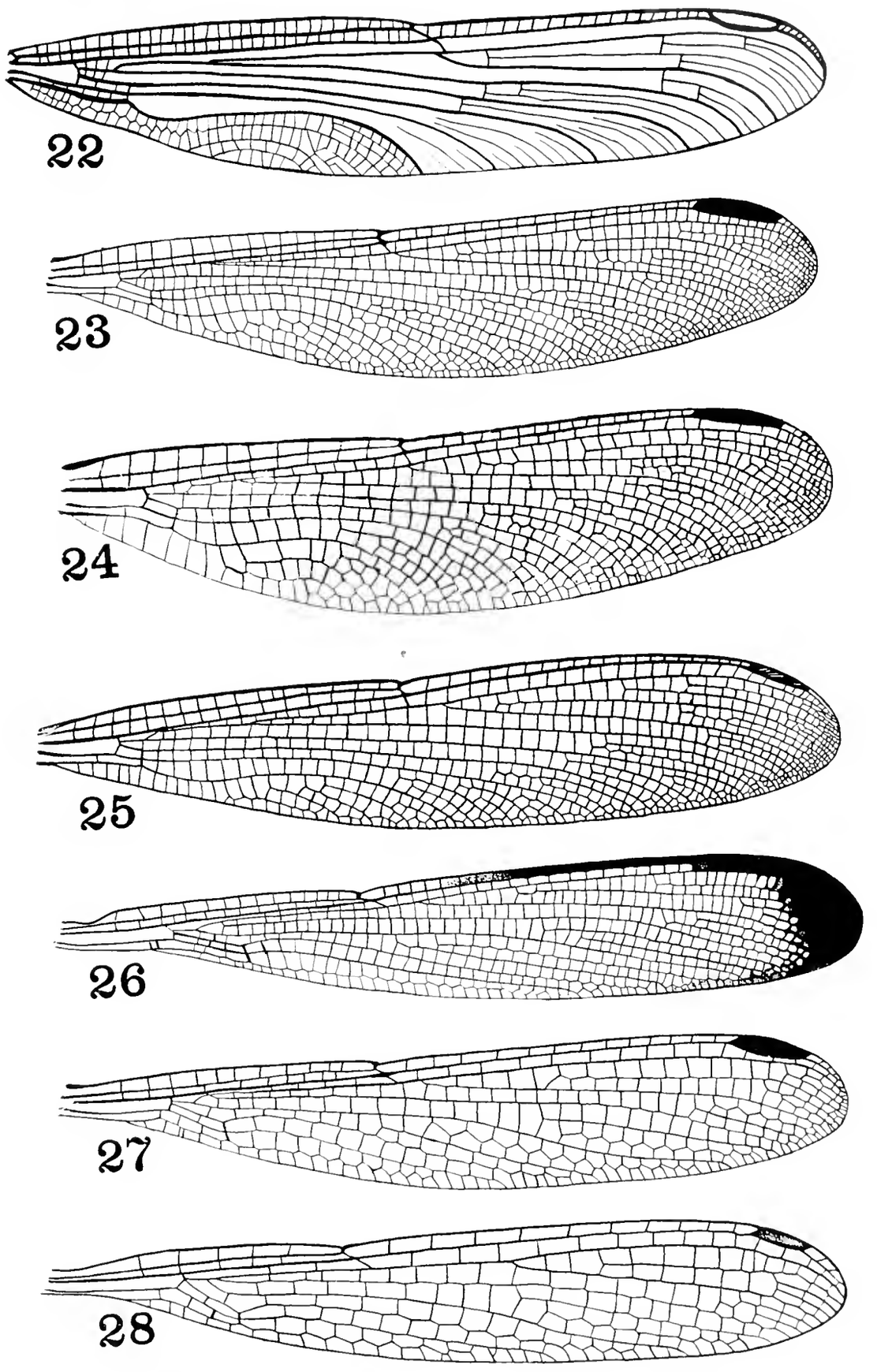

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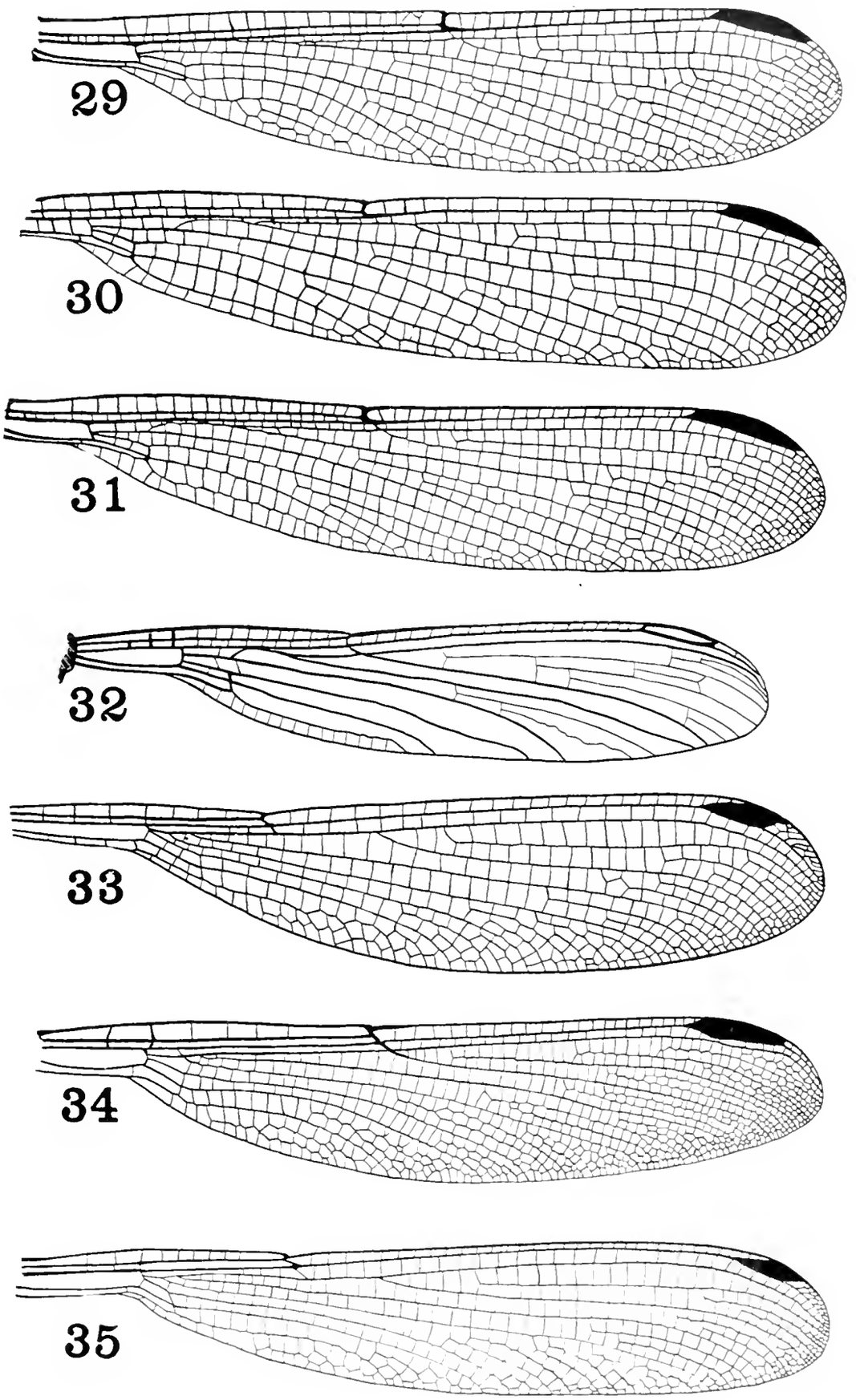

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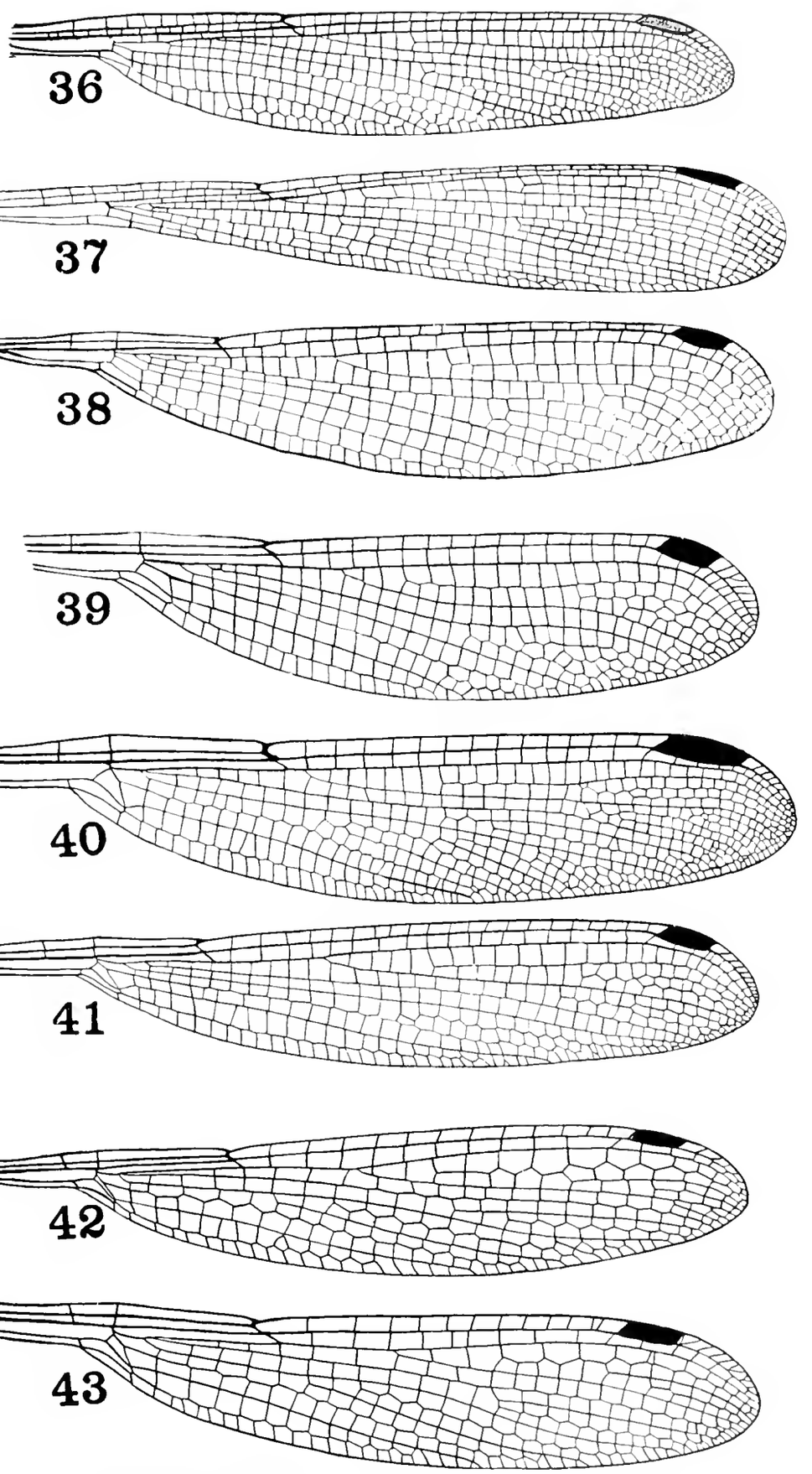

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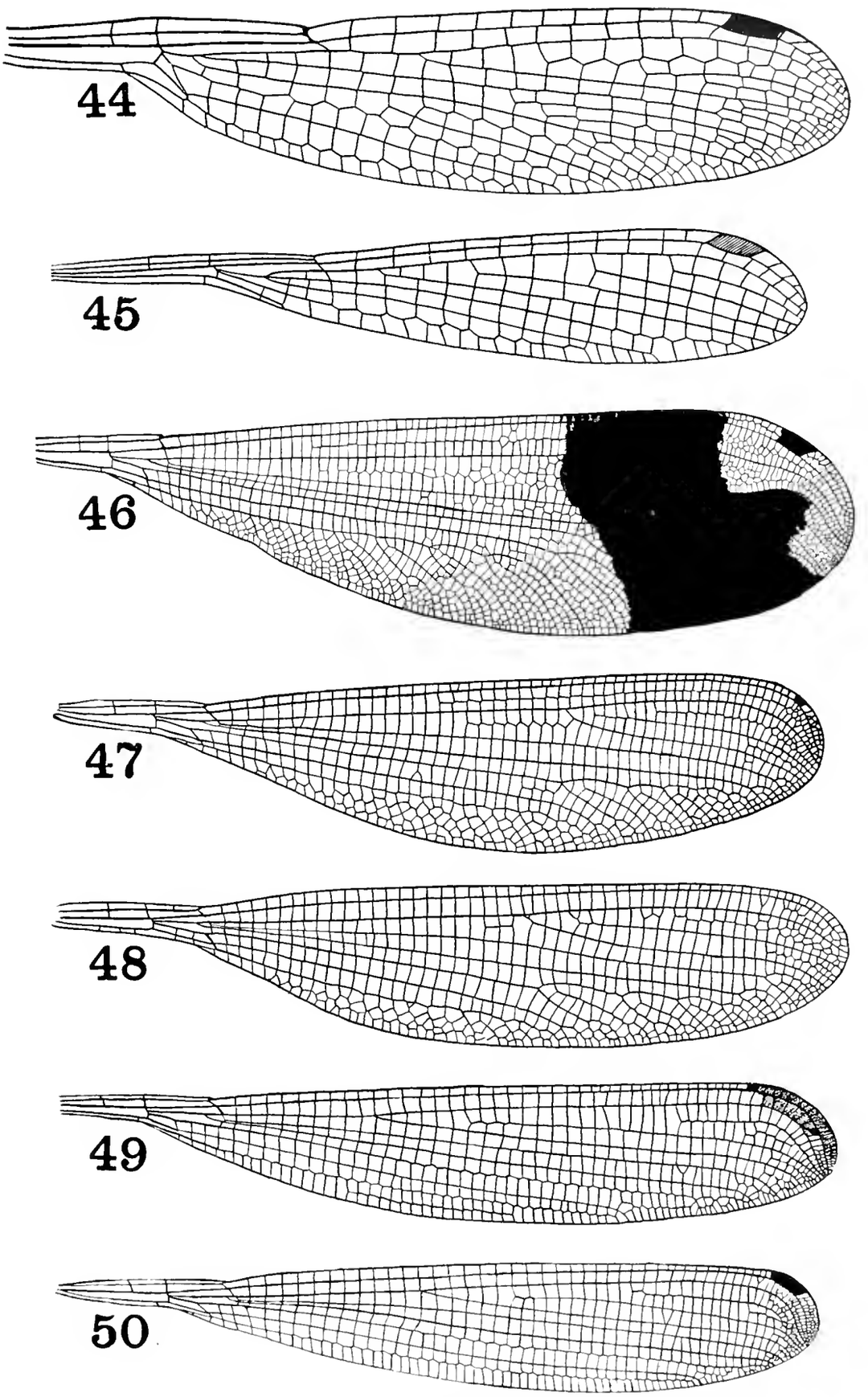

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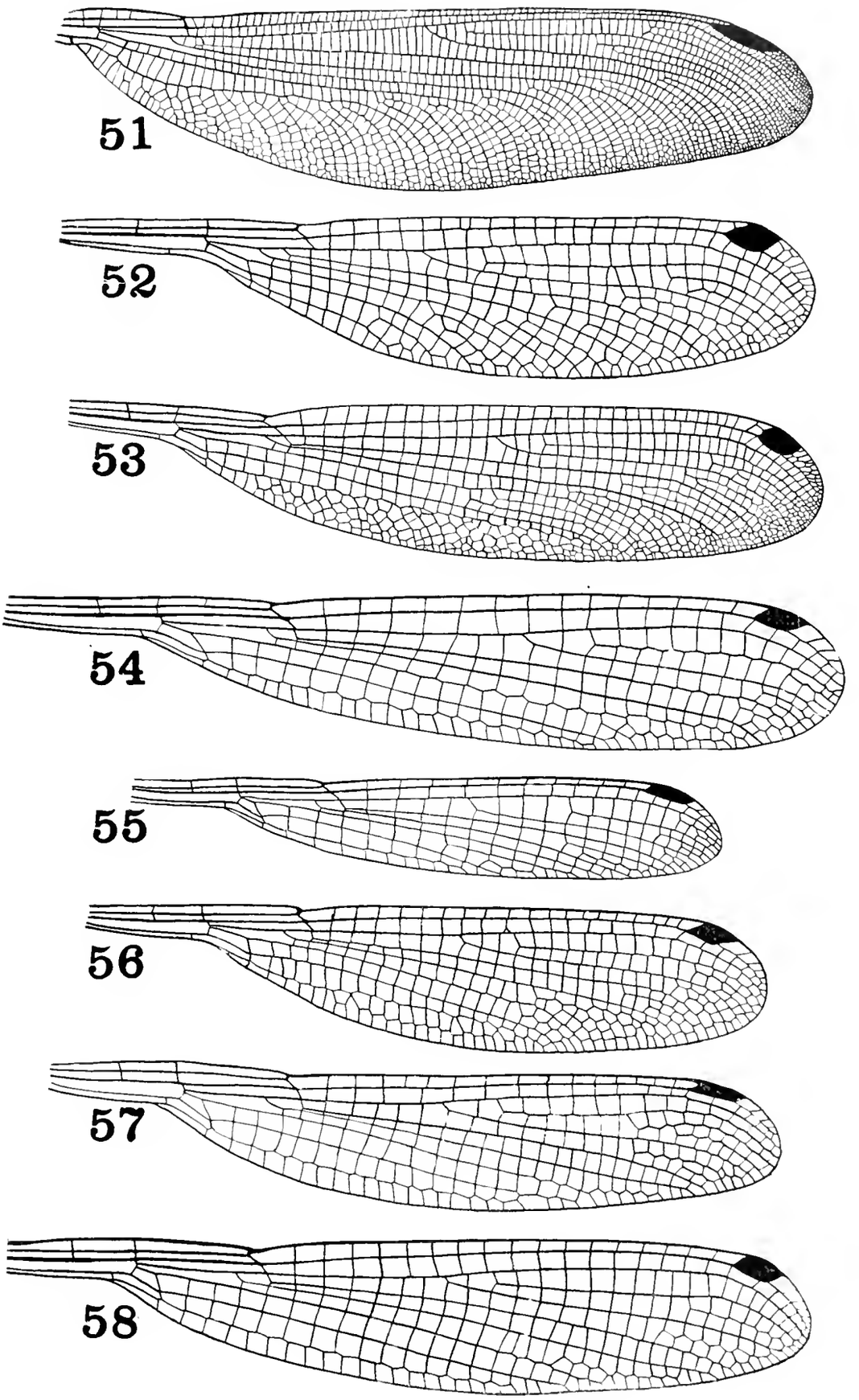

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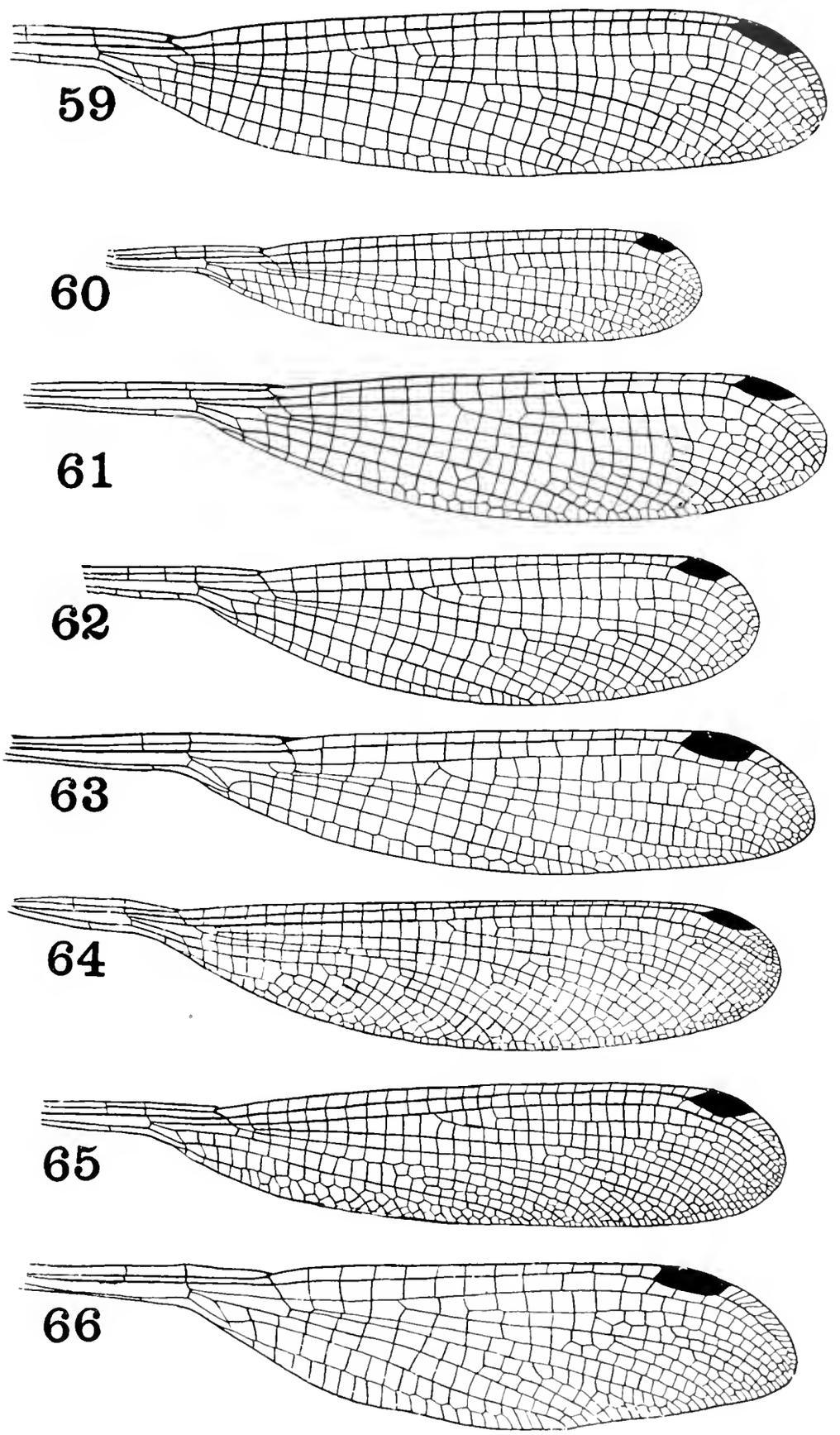

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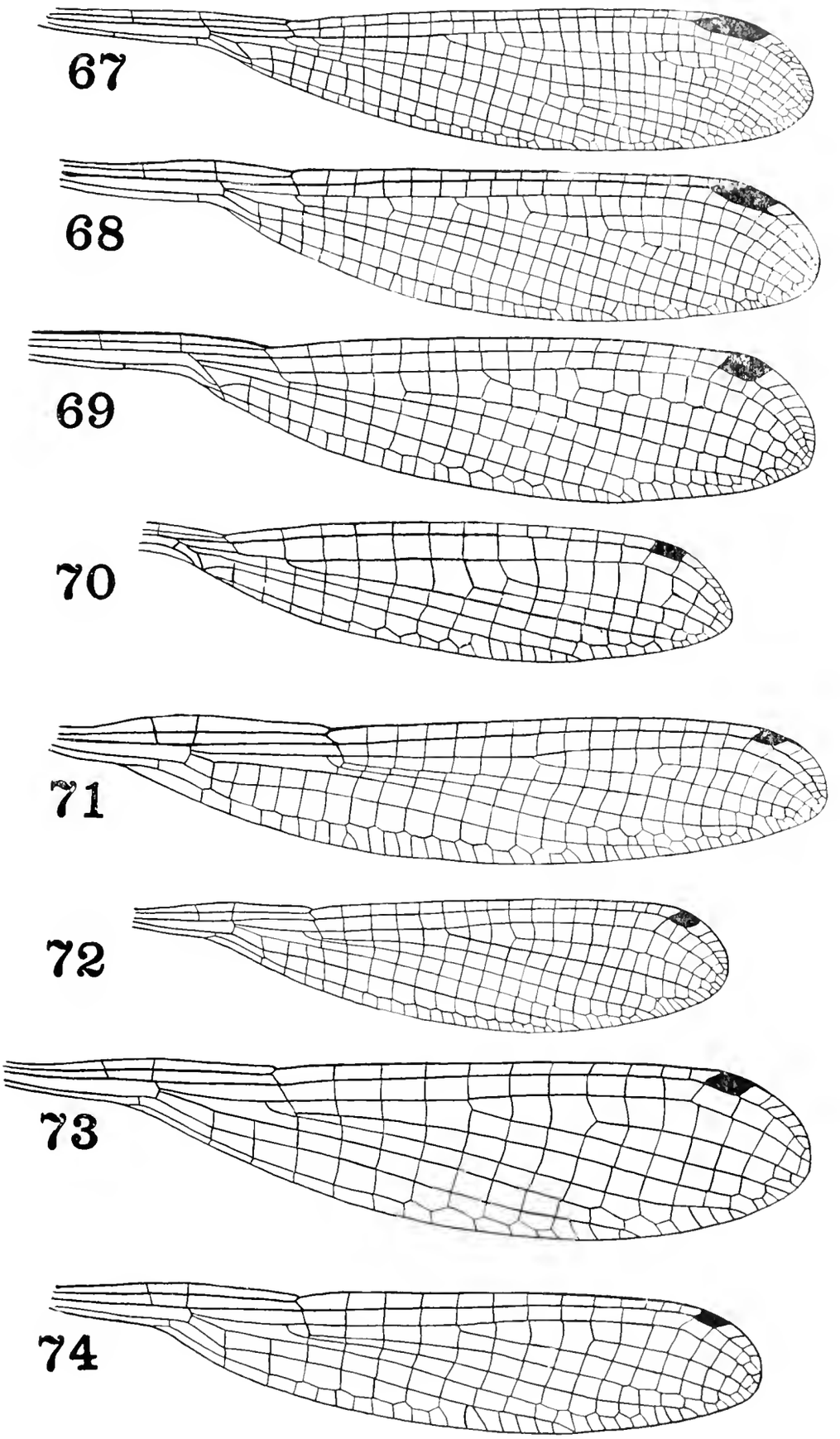

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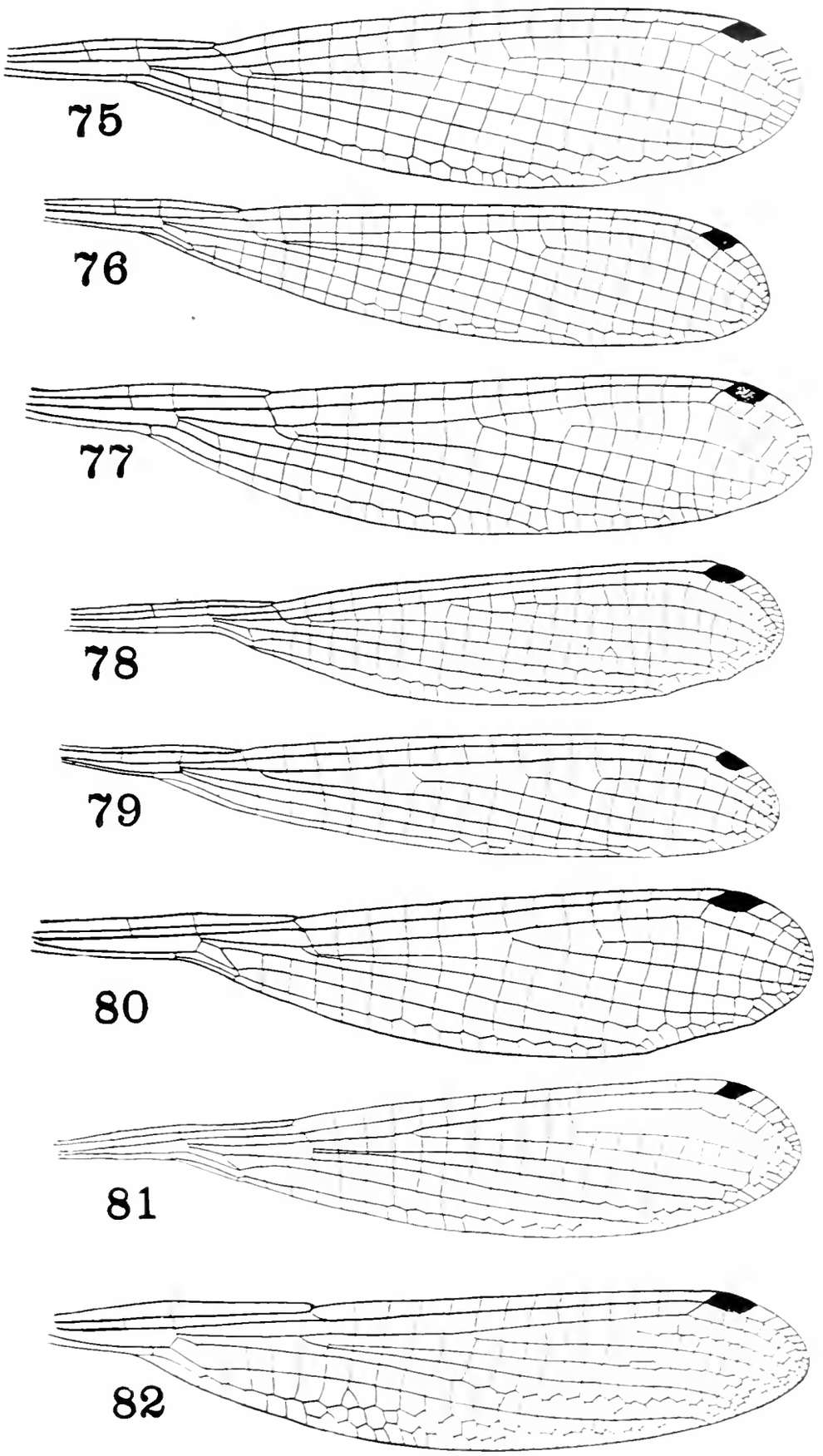

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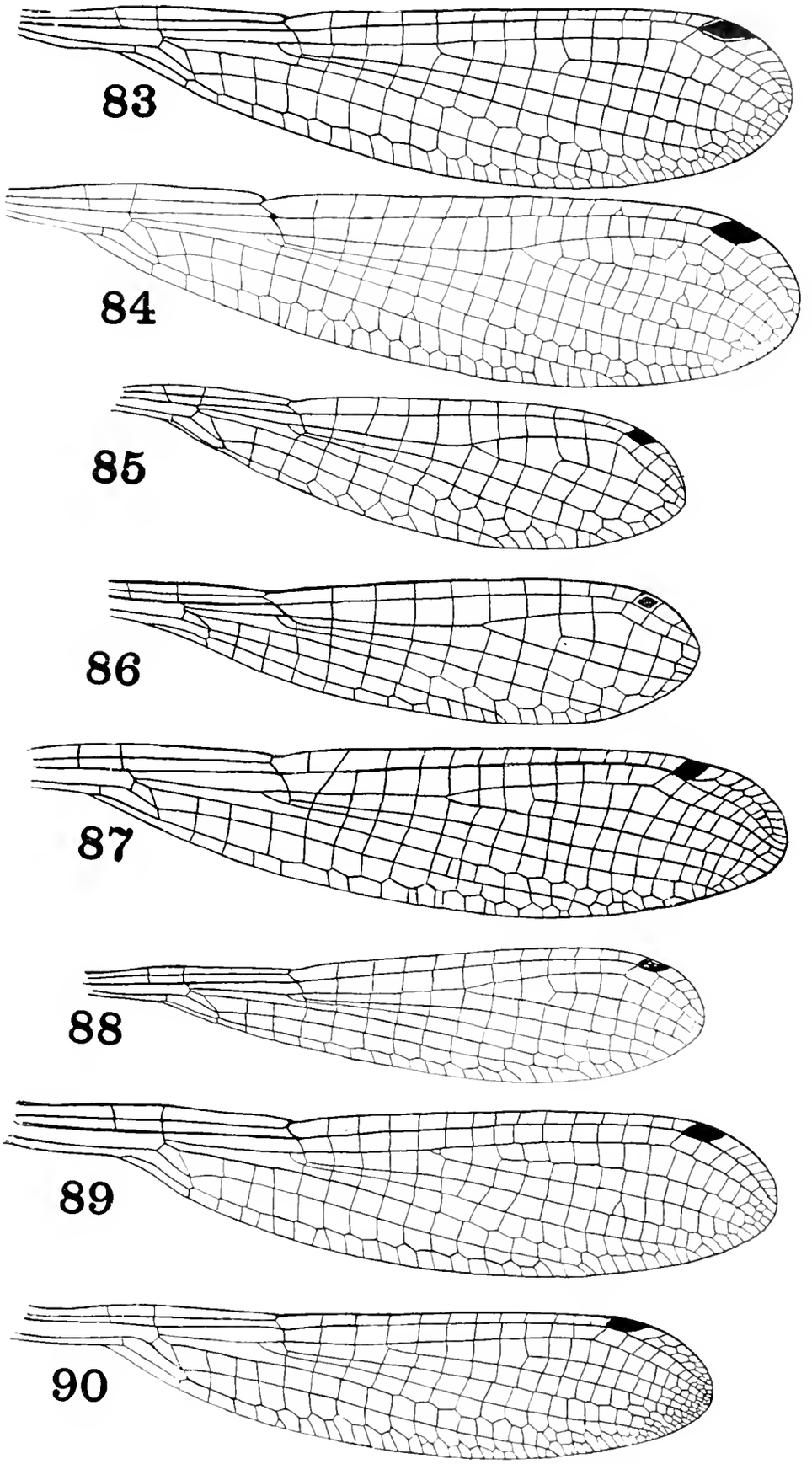

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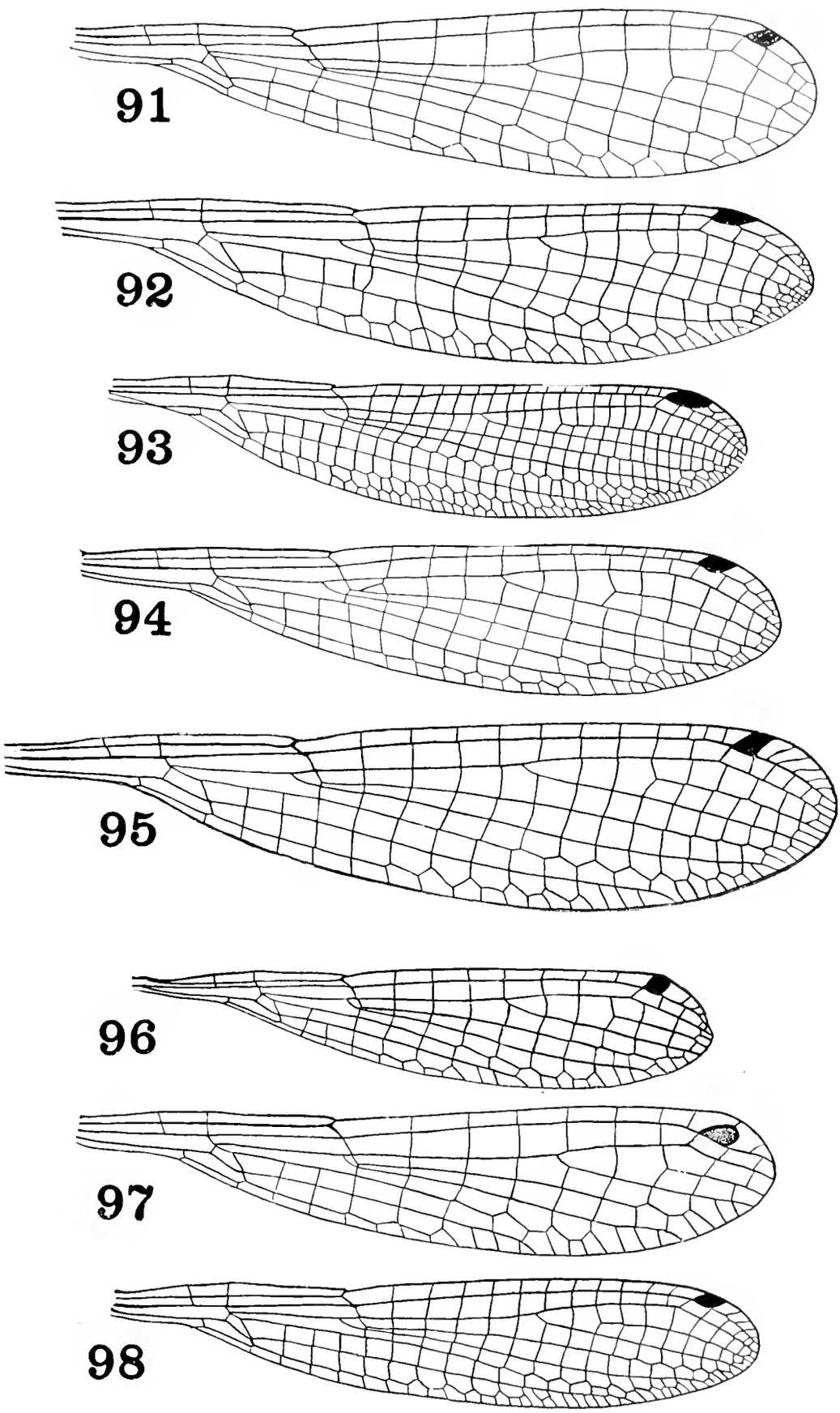

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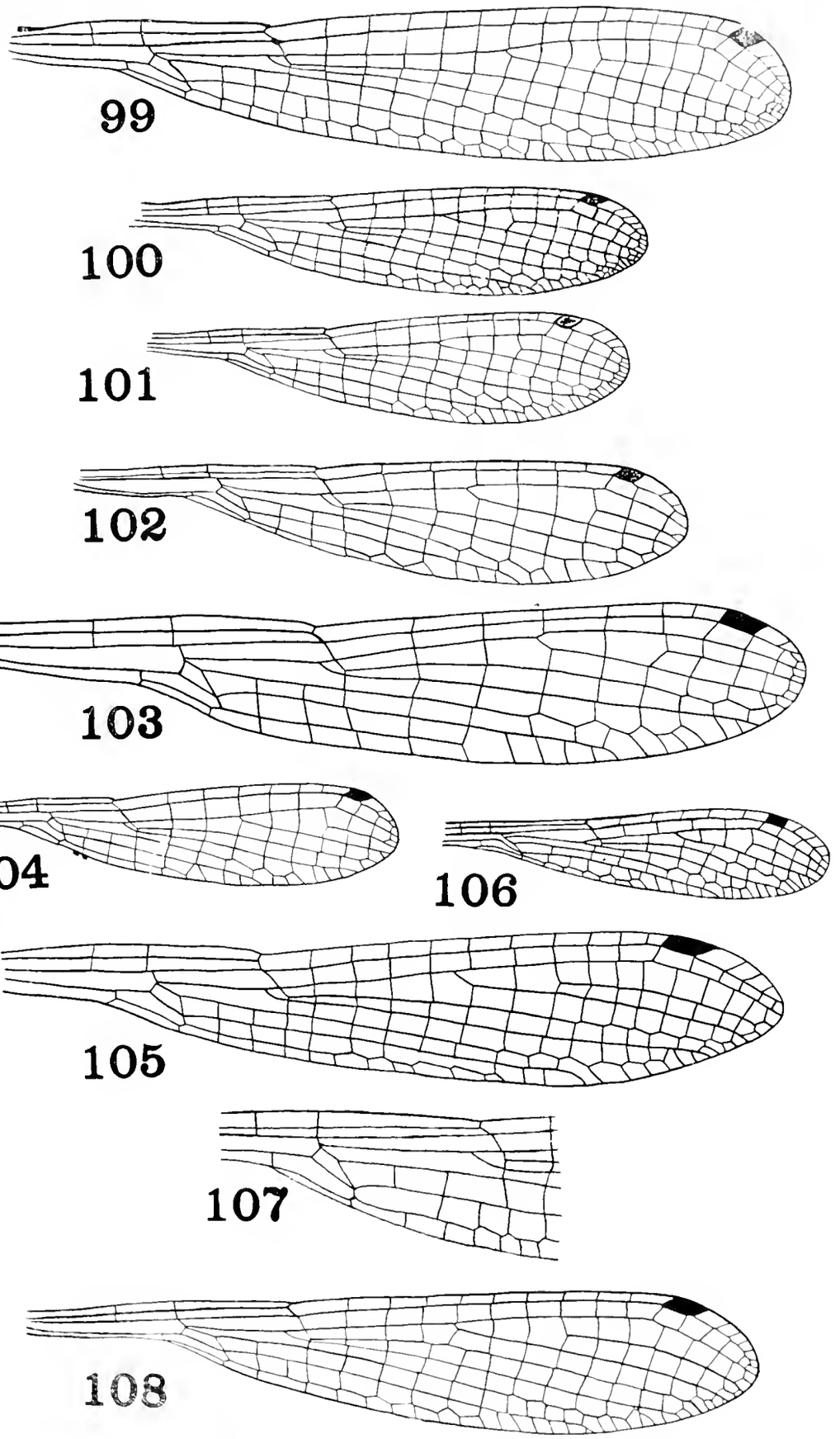

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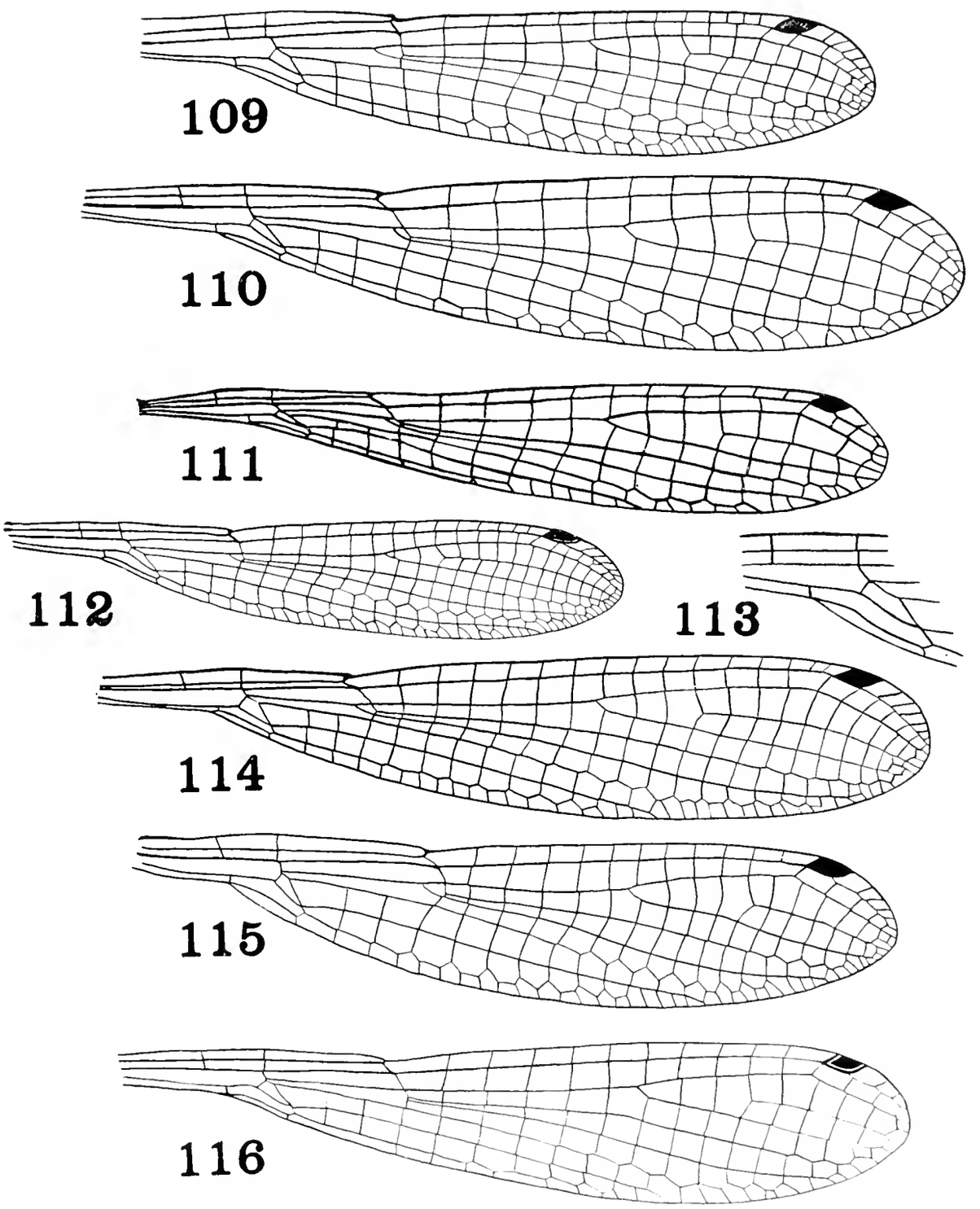

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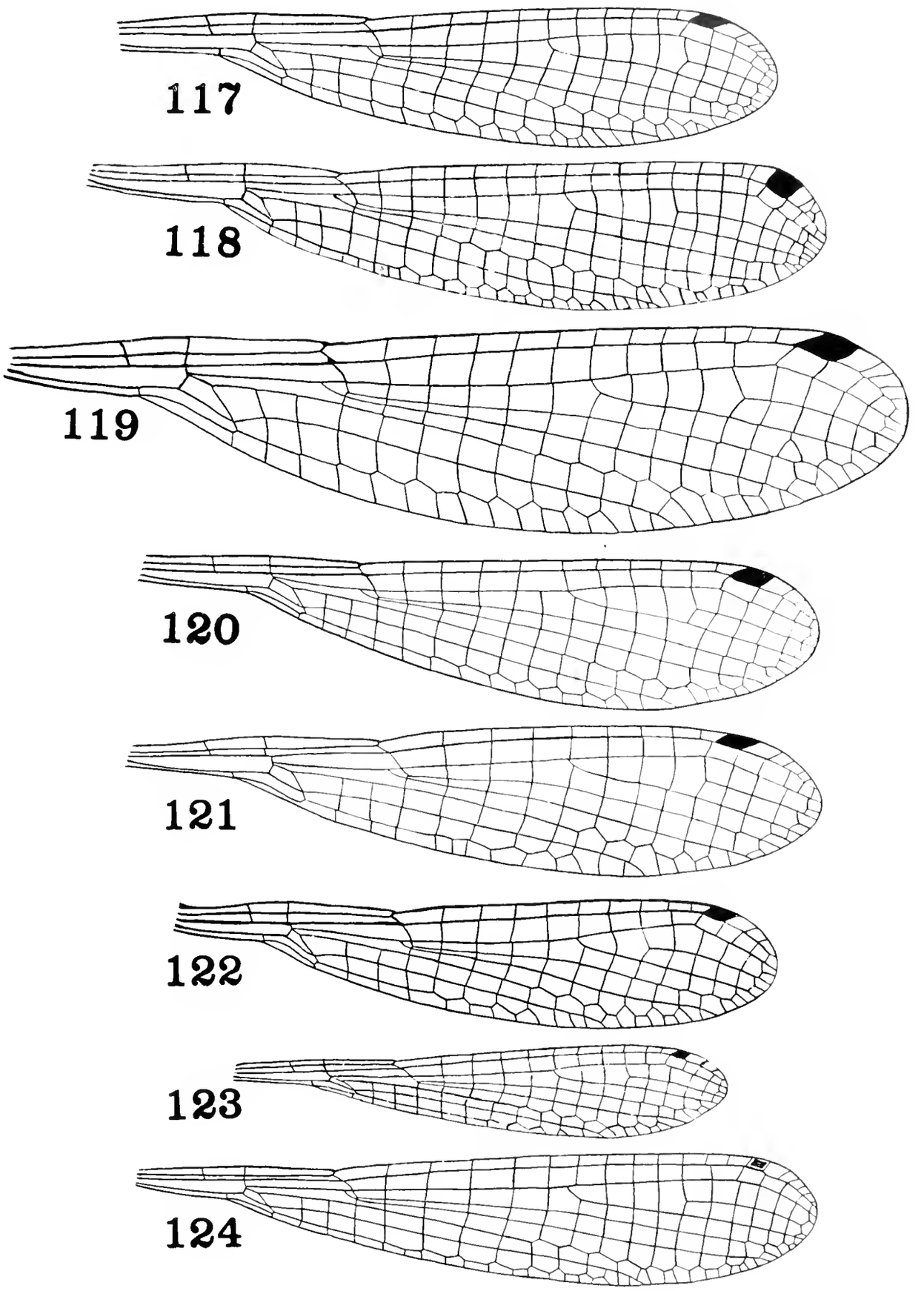

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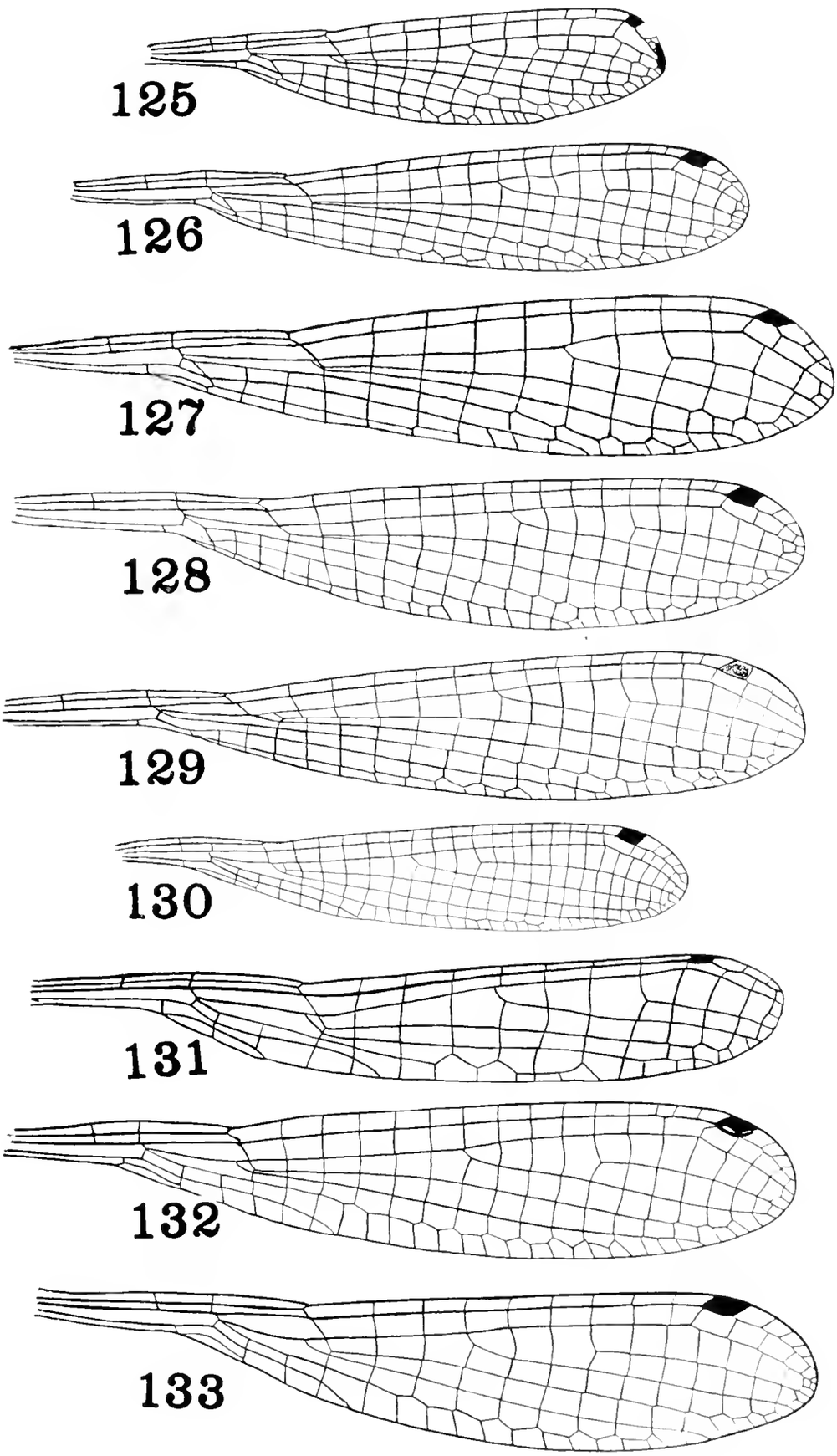

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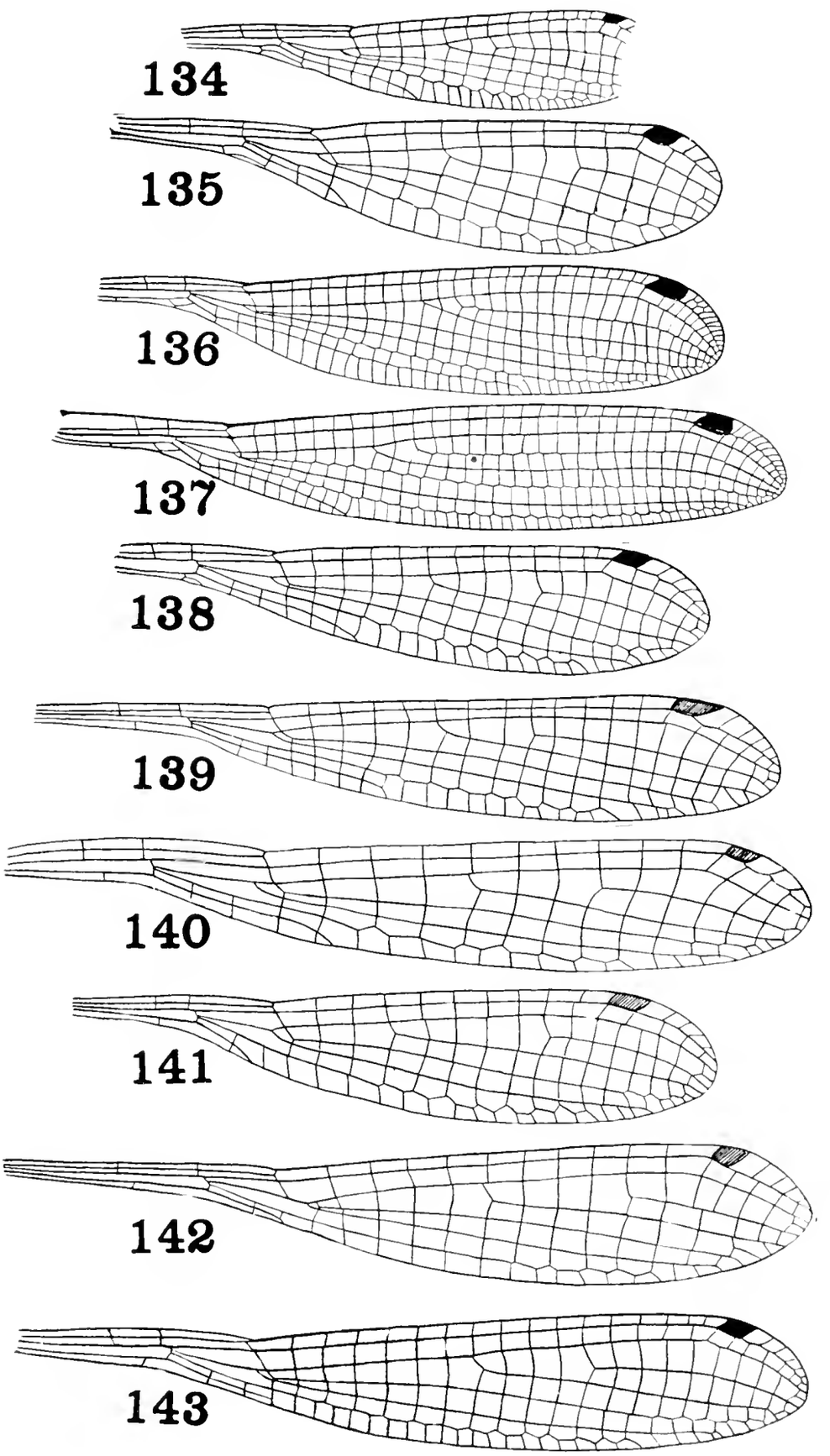

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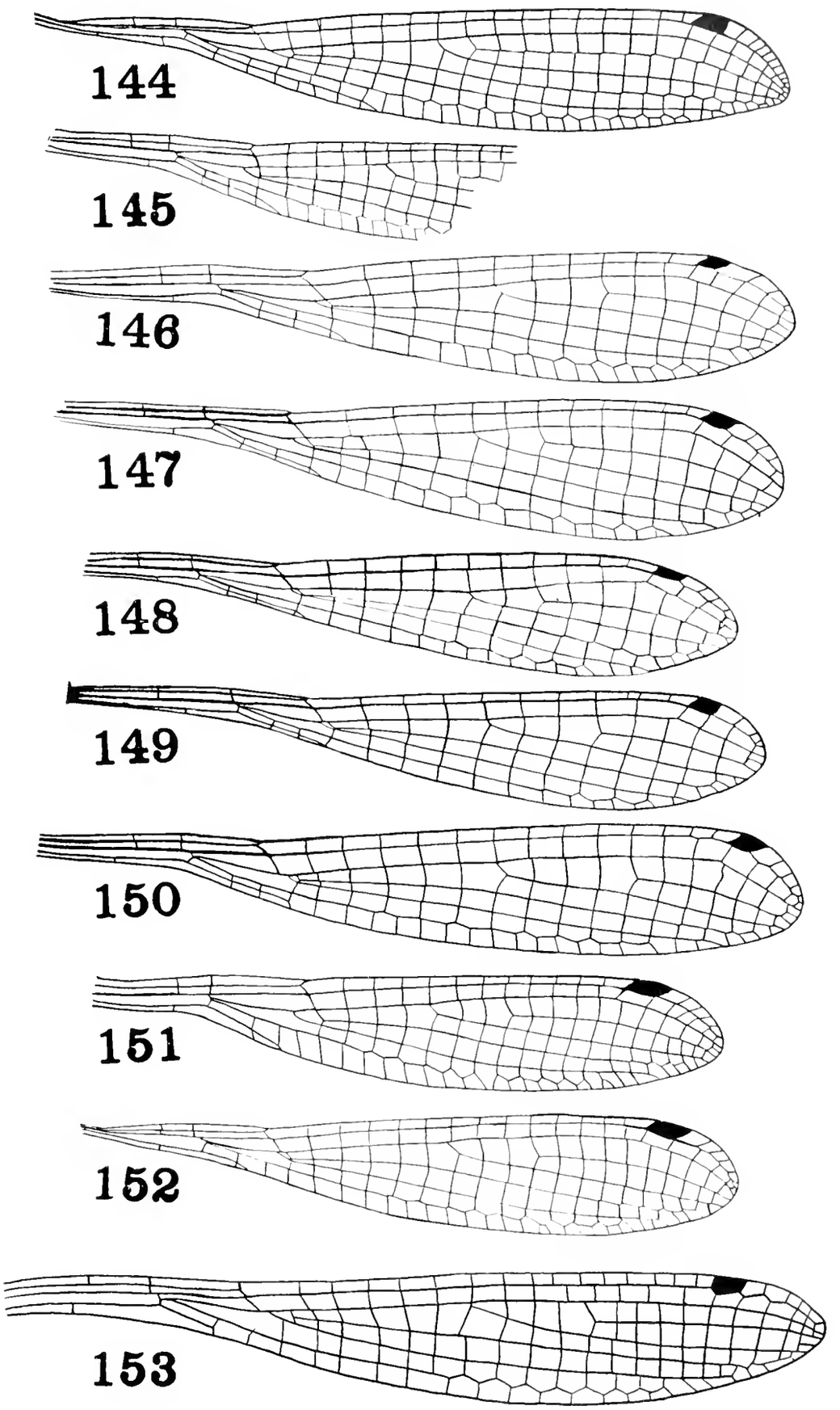

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