A GENEALOGIC STUDY OF DRAGON-FLY WING VENATION.

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INTRODUCTION.

This is a new study of one of the oldest subjects in entomology. It is an application of the methods of comparative morphology to the interpretation of some external characters universally employed in systematic work upon insects.

The richly veined wings of dragon-flies have been carefully studied by many able entomologists; their interesting peculiarities are well known; the homologies of the various parts of the wing have been determined throughout the order; and there already exists a considerable body of evidence as to the nature and extent of variation in venational characters. There has been as yet no serious effort to use these characters to determine genealogic succession within the order. It is the main purpose of this paper to translate the records of natural selection as written in the abundant characters of these wings.

At the outset I wish to acknowledge my indebtedness to the following gentlemen, who have all aided me generously: To Prof. J. H. Comstock, of Cornell University, I am indebted first of all for constant advice throughout the progress of this study; to Mr. Samuel Henshaw, of the Museum of Comparative Zoology, for free use of the Hagen Collection of Odonata during a stay of two months in Cambridge; to Dr. R. T. Jackson, of Harvard University, for similar privileges in the study of the fossil Odonata of the same museum; to Dr. P. P. Calvert, of the University of Pennsylvania, for the loan of valuable specimens; to Monsieur R. Martin, of Le Blanc, for the gift of specimens; and to Dr. S. H. Scudder, for the privilege of examining the types of fossil Odonata in his collection, and also some of his original unpublished drawings.

I. THE ONTOGENY OF THE VENATION.

Historical.

It is pleasant to find that the first contribution to the knowledge of developing veins was made by Dr. Hagen. In 1846 he published a little paper, a page in length, entitled Ueber die Bildung des Geäders der Libellen-flügel.[a] In this he wrote that by simply rubbing the expanding wing of a transforming dragon-fly between the thumb and finger the two membranes of the wing may be slipped apart, and it will be readily seen that the venation is double, i. e., developed alike in both membranes, and that the double network thus formed is united and exactly coincident along the courses of the wing tracheæ. At this day one who wishes to see the relation of veins to tracheæ can hardly do better than repeat this simple experiment. Thus he may at least see, a thing too little comprehended hitherto, that the tracheæ passing out from the body cavity into the wing cavity are essentially internal organs as compared with the cuticular (hypodermal) thickenings formed about them constituting the veins.

Oswald Heer appears to have been the first to use the wings of dragon-fly nymphs as an aid to interpreting the homologies of the adult venation.[b] He made no use of tracheæ, however, but only of the veins marked upon the exterior of the wing sheath, these being essentially the same as the veins in the adult only served to confirm him in an erroneous interpretation of homologies.

Roster first figured the tracheation of a nymphal wing.[c] His figure (of *Æschna cyanea*) was made to show tracheal distribution without reference to venation. It is in several points incorrect, and a chance remark in the text shows that Roster did not perceive the order which exists in the arrangement of the tracheæ.[d]

In 1888 Brauer and Redtenbacher published a paper on immature insect wings, using mainly a species of Æschna to show the fallacy of Adolph's theory of alternating convex and concave veins.[e] Of the

[a] Stettiner Ent. Zeit., VII, pp. 115–116. A similar paper by Dr. Hagen, Kurze Bemerkung ueber das Flügelgeäder der Insecten (Wien. Ent. Zeit., V, pp. 311–312), was called out in 1886 by the theories with which Adolph and Redtenbacher had encumbered their useful works upon the homologies of the wing veins in general. Then in 1889 he published (Spaltung eines Flügels um das dopplete Adernetz zu zeigen, Zool. Anz., XI, pp. 377–378) a similar article with a figure, showing the main facts set forth in all these papers.

[b] Heer, Oswald, Die Insectenfauna der Tertiargebilde von Oeningen und von Badoboj in Croatien, Neue Denkschr. Schweiz. Ges., XI, 1850, Libellulidæ, pp. 36–89, pl. IV.

[c] Roster, D. A., Contributo all 'anatomia ed alla biologia degli Odonata, Bull. Soc. Ent. Ital., XVII, pp. 256–268, 2 pls.

[d] Mandando in questo percorso cinque o sei diramazioni che innervano *intrecciandosi in vario modo*, la superficie dell 'ala. [The italics are mine.—J. G. N.]

[e] Ein Beitrag zur Entwickelung des Flügelgeäders der Insecten, Zool. Anz., XI, pp. 443–447.

branches of a single main trachea, some were shown to be incorporated into convex and some into concave veins. Thus disappeared the fundamental difference which had been assumed to exist between the two kinds of veins.

Brauer and Redtenbacher also affirmed that the homology of veins in remotely related insects is only to be determined by the study of their development—a suggestion which has until quite recently been generally commended in theory and more generally disregarded in practice.

Brogniart, in his Etude sur la nervulation des ailes des insectes,[a] figures both the tracheation and the venation in careful detail, and points out the close correspondence between the two. He fails to recognize the individuality of the veins and tracheæ, however, designating mere branches as independent veins, and he confuses the identity of one branch (*Rs*) by giving it a different designation in the two stages.

The foregoing papers have shown (without expressly stating) the following points: (1) The precedence of the tracheæ and the subsequent development of the veins about them, through hypodermal elevations becoming paired troughs, which by fusion become hollow tubes inclosing the tracheæ; (2) the difference in kind, and (3) the correspondence in arrangement between the two structures; and (4) the fact that simpler conditions are found in the earlier stages.

I have traced the development of the venation through a series of nymphal stages and have published recently, in collaboration with Professor Comstock, a preliminary account of it,[b] but must for present purposes review the matter more at length.

ONTOGENY IN GOMPHUS DESCRIPTUS.

For the present I pass by all points of histological structure, not as being uninteresting or unimportant, but as being unessential to the specific problem now in hand. I shall deal in this paper with facts that may be observed without the aid of sections, and, for the most part, with no special preparation whatever.[c]

Six principal tracheæ traverse the wing of a dragon-fly in all stages. These arise very early in the budding wing, springing separately from a longitudinal thoracic tracheal trunk which makes a slight bend outward to meet the base of the wing. These tracheæ and their cor-

[a] Recherches sur les insectes fossiles, etc., Paris, 1894. See especially pp. 204–208, and pl. VIII.

[b] Comstock, J. H., and Needham, J. G., The Wings of Insects, Amer. Nat., XXXII and XXXIII, 1898 and 1899; Art. Odonata, XXXII, pp. 903–911, 9 figs.

[c] The only preparation necessary to demonstrate the facts cited in the following pages is that of the wings of nymphs, which should be removed fresh, mounted quickly in glycerin jelly, and cooled suddenly (to retain the air in the tracheæ), and are then ready for observation.

responding veins will be designated, beginning at the anterior margin of the wing, by the following names and abbreviations:

1. *Costa* (*C.*).
2. *Subcosta* (*Sc.*).
3. *Radius* (*R.*).
4. *Media* (*M.*).
5. *Cubitus* (*Cu.*).
6. *Anal veins* (*A.*).

Typical branches will be designated by added numerals (as M_1, M_2, M_3, and M_4, designating from front to rear the branches of the media), except the posterior division of the radius, which has received the special name of "radial sector" (*Rs.*). Accessory and secondary branches will be designated by small letters added in the order of their development of the branches (as Rs_a, Rs_b, Rs_c, etc., for the secondary branches of the radial sector).

Fig. 1 represents the tracheæ in two early stages of the development of the nymphal wing of *Gomphus descriptus*. *A* is from a nymph less than one-fourth grown, the wing 1 mm. long. The tracheæ so closely resemble those in the developing wings of insects of many other orders there can be no doubt as to their homology. The radial sector is

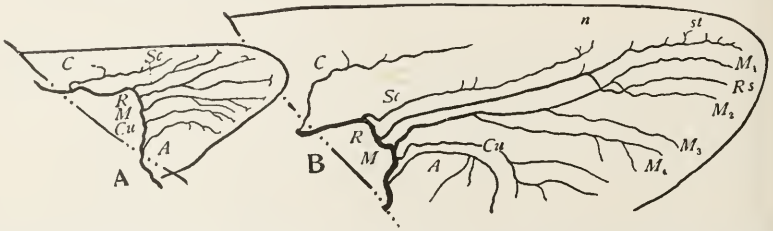


FIG. 1.—TRACHEATION OF THE WINGS OF TWO NYMPHS OF *Gomphus descriptus* BANKS, TWO EARLY STAGES. FOR EXPLANATION OF LETTERING SEE TEXT; ALSO, *n* = NODUS AND *st* = SUPERTRIANGLE.

simple—it is generally branched in other orders—and there is a single anal vein. In other orders there are oftenest three.[a] Otherwise the tracheæ are entirely typical at this stage. It is worthy of note that at this stage the wing is somewhat bilaterally symmetrical and the tracheæ are of almost equal size and length.

Fig 1. *B* is from an older nymph with wings 3 mm. long. The two marginal tracheæ are reduced or, rather, outstripped by their competitors, the wing has become quite unsymmetrical, and the radial sector has come to lie across the distal end of the media.

Fig. 2 represents the tracheation of both fore and hind wings of a grown nymph of the same species. The costal trachea is so dwarfed as hardly to enter the costal vein. The radial sector lies back of the two anterior branches of the media which it crosses. The other tracheæ, also, are assuming their definitive positions, and some of them are becoming strongly angulated at the middle and toward the base of the wing.

These three stages show clearly how the primitive insect wing has

[a] Probably the three terminal branches of this trachea represent the typical first, second, and third anal tracheæ fused together.

been modified to produce the Odonate type, in which the most anomalous thing is the crossing of the radial sector over two branches of the media. I can not now suggest even a possible reason why this should have taken place. It is apparently a character quite distinctive of the order Odonata.

A photograph of fore and hind wings of a grown nymph of the same species, showing the tracheæ and the veins together as they appear during the last nymphal stage, is reproduced in Plate XXXI, fig. 1. This will assist greatly in comparing the adult wings shown in fig. 3 with the preceding figures. This also shows that certain well-known features of the dragon-fly wing are due to strong cuticularisation

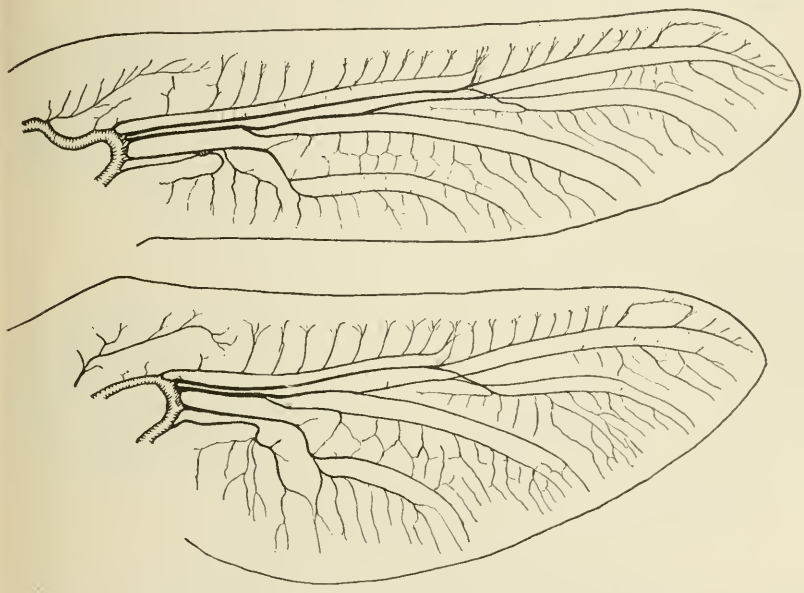


FIG. 2.—FORE AND HIND WINGS OF A GROWN NYMPH OF *Gomphus descriptus*, SHOWING TRACHEÆ. THE PERMANENT VENATION WHICH SHOWS DISTINCTLY AT THIS STAGE IS OMITTED.

between the tracheæ. Such are the stigma (*st.*), the nodus (*n.*), and parts of the arculus (*ar.*) and triangle (*t.*).

The radial sector.—In the adult wing (fig. 3) the radial sector appears to be a branch of the media. It has always been so interpreted. The only indication of its connection with the radius is the persistent obliquity of an apparent cross vein between veins M_2 and *Rs*. This is in fact not a cross vein, but a part of the radial sector, while the longitudinal trunk (*br.*) extending proximally from this point to connect vein *Rs* with vein M_{1+2}[a] is not homologous with any principal vein, but is a secondary structure developed for mechanical advantage. There will be seen in the plate a recurrent tracheal twig preceding this structure.

[a]The plus sign is thus used as a convention for indicating united branches or tracheæ, the numerals it connects designating the branches conjoined.

Areulus and triangle.—The radius and the media tend from the first to unite at the base, and in the adult wing appear to form a single vein as far as the areulus. But even in the adult wing this vein may be seen, as pointed out by Brogniart, to be composed of two, whose union he aptly compared to that of the barrels of a gun. Media suddenly bends away from the radius and is met by a cross vein from the cubitus, and thus the areulus is formed. A similar deflection of the cubital tracheæ just beyond the areulus makes a place for the development of the triangle, which is completed by two cross veins approximated upon vein M_4. Thus only the upper end of the areulus and the inner side of the triangle are formed from principal veins.

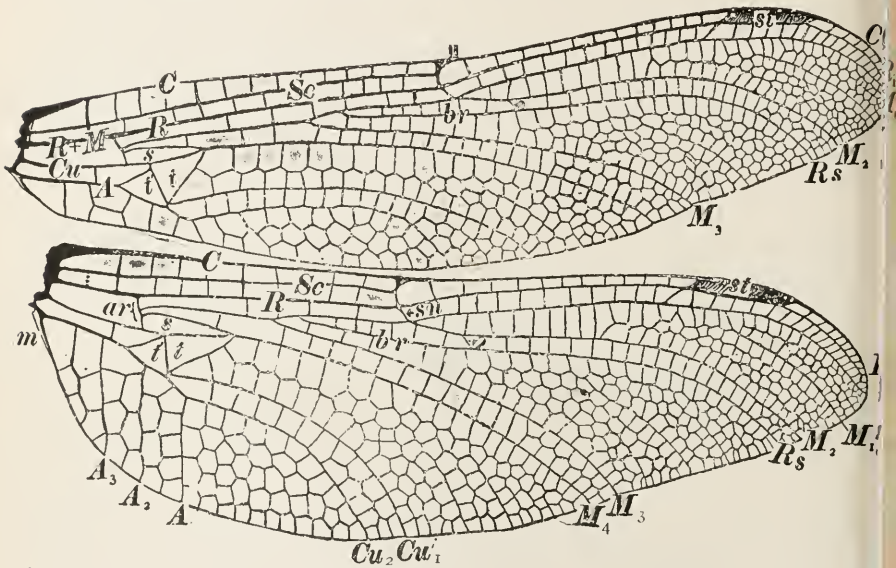


FIG. 3.—VENATION OF THE IMAGO OF *Gomphus descriptus*.

Tracheæ and cuticular thickenings thus combine to produce a unique insect wing, whose chief peculiarities arise from three transverse unions of its veins, at stigma, nodus, and areulus, respectively. Added to the usual thickening of veins and corrugation of membrane at the front border, these three unions make the part of the wing which cuts the air and supports other parts very strong. It will be observed that at the stigma but two or three veins are thus conjoined, at the nodus, more, and at the areulus (by means of parts accessory to the areulus) all the principal veins are bound together across the basal part of the wing. A line drawn from the outer end of the stigma to the hind angle of the triangle divides the wing into two areas, the anterior of which includes the strong framework of the wing, while the other is yielding membrane with weak venation, adapting the wing for that rapid sculling action in air by which forward motion is produced.

II. THE STUDY OF THE WING BY AREAS.

These three points of transverse bracing are also the points about which have played the forces which have evolved the dragon-fly wing. They are the points about which one can best follow the shifting of veins and tracheæ. In a study of genealogy one can hardly do better, therefore, than to discuss the wing by areas with these points as centers, drawing freely upon ontogeny, comparative anatomy, and paleontology for evidence of the changes that have taken place.

THE AREA OF THE STIGMA.

The stigma is developed upon the cutting edge of the wing at the point of greatest impact against the air. It would seem to serve the

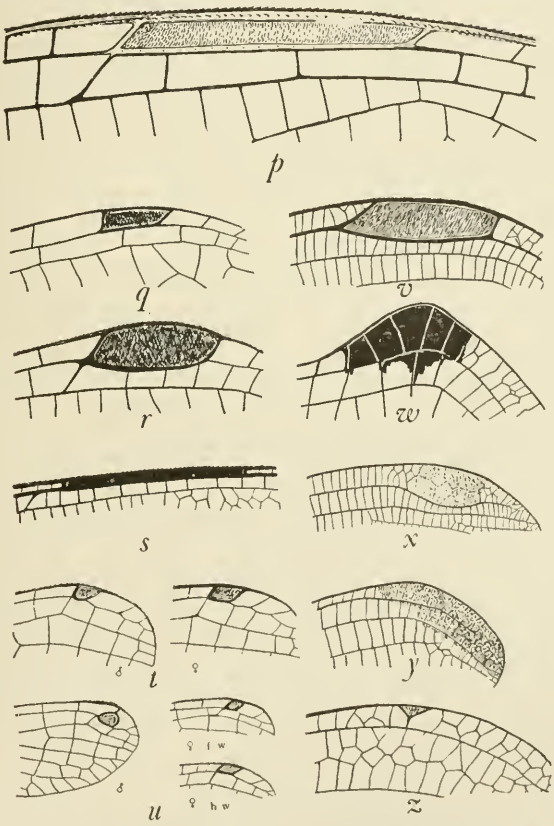


FIG. 1.—PTEROSTIGMAS; *p*, OF *Anax junius* DRURY; *q*, OF *Miathyria marcella* SELYS; *r*, OF *Neogomphus molestus* SELYS; *s*, OF *Uropetala carovei* SELYS; *t*, OF *Agrion mercuriale* CHARPENTIER; *u*, OF *Anomalagrion hastatum* SAY; *v*, OF *Thore gigantea* SELYS; *w*, OF *Mecistogaster lucretia* DRURY; *x*, *Calopteryx maculata* BEAUVOIS; *y*, *Microstigma* SP?; *z*, *Microstigma rotundatum*, SELYS, HIND WING.

double purpose of firmly uniting the veins of the front margin and of increasing the efficiency of the wing stroke by adding weight at this

striking point. Its shape and extent vary considerably and are often characteristic of groups; but the stigma seems not to contain in itself such characters for the critical determination of the course of specialization as are furnished by surrounding parts.

In the wings of the more generalized members of several families of Odonata there is between veins R_1 and M_1 a series of cross veins, several of which fall directly under the stigma, and all of which are nearly or quite perpendicular to the veins they connect. One of these cross veins which happens to lie at the proximal end of the stigma waxes stronger than its fellows, and is set in an oblique position in such way as to strongly brace the stigma against vein M_1. Three not remotely related Gomphinæ will illustrate the stages in the development of this strong brace from an ordinary cross vein. In *Epigomphus paludosus* (fig. 8) the proximal end of the stigma has no cross vein exactly in line with it; in *Cyclophylla diphylla* (Plate XXXIV, fig. 1) it is in line, but little strengthened; but in *Gomphus dilatatus* (Plate XXXIII, fig. 1) it has become a strong and evident brace. A parallel series might be pointed out among the Æschninæ (compare such genera as *Staurophlebia* (Plate XXXIX, fig. 2), *Basiæschna* (Plate XXXVII, fig. 2), and *Gynacantha* (Plate XXXIX, fig. 3), and the Agrioninæ offer another parallel, with the addition of an interesting feature, which is illustrated by a series of such genera as *Lestes* (Plate LIII, fig. 1), *Philogenia* (Plate LIII, fig. 4), *Argia* (Plate LIII, fig. 5), and *Nehallennia* (Plate LIV, fig. 8). In this series there is the same development of a brace from a cross vein; and, correlated therewith, a progressive angulation of vein M_1 at the base of this cross vein, forming a triradiate brace at that point.

An entirely different method of bracing the front of the wing at the stigma has prevailed in a few forms (*Thore*, fig. 4, *v*, etc.). The cross vein below vein R_1 is not utilized, but the two veins bounding the proximal and posterior sides of the stigma are deflected so as to meet vein R_1 in a strong Y-shaped brace, which, doubtless, serves a purpose analogous to that served by the other triradiate brace described above.

Fig. 4 shows at *p* the normal stigma of *Anax junius*, greatly enlarged. It shows, also, a few common forms of stigma, both braced and unbraced (*q* to *t*), and a few uncommon and more or less degenerate forms (*w* to *z*), which will be discussed under another heading.

THE REGION OF THE NODUS.

Here at once we come upon very peculiar wing features.

The nodus is the stout cross vein near the middle of the costal border of the wing, joining the costa, the subcosta, and the radius. It is traversed by a more or less evident suture, making a flexible and elastic joint which, without loss of strength in the parts which need

rigidity, would seem to allow more effective flexion of the distal parts of the wing.[a]

We have already seen the trachea *Rs* descending at the nodus and crossing tracheæ M_1 and M_2. The veins formed about these tracheæ bind them all solidly together. For convenience of reference we now designate that portion of the radial sector which unites the lower end of the nodus with the median vein as the *subnodus* (*sn.*) and the short oblique portion of the radial sector appearing as a cross vein behind vein M_2 as the *oblique vein* (*o*), and the trunk secondarily developed to connect the radial sector proximally with vein M_{1+2} as the *bridge* (*br*).

In the suborder Anisoptera we may then note that the radial sector fuses with vein M_2 for a little way, carrying the oblique vein a variable distance beyond the subnodus. The bridge is outlined in tracheæ of two very different types, which are almost characteristic of the two families of the suborder. (1) In all the Æschninæ of which I have had nymphs for examination the antecedent trachea is simple, and springs from the radial sector near what will be the distal end of the bridge (fig. 5) and extends in a direct line proximally toward vein M_{1+2}. (2) In most Libellulidæ the trachea which precedes the bridge springs from the radial sector near the origin of the latter (fig. 6), descends to the level of the bridge that is to be, forks, and sends its branches in opposite directions to meet veins M_{1+2} and *Rs* respectively. In the Macromiinæ, however, it is formed by a modification of the latter type, as shown for *Didymops transversa* in fig. 7 A. Fig. 7 B shows how, by a further division of the radial sector near its base, two oblique veins are formed in the Cordulegasterinæ and Petalurinæ. Compare also with fig. 28.

In the suborder Zygoptera, so far as known to me, trachea *Rs* appears as a branch of the media, the subnodus, while formed in the usual place, being destitute of a tracheal trunk. The Zygopterous nymphal wing figured herewith (Plate XXXI, fig. 2) shows that the trachea *Rs* has, in this (well grown) stage, at least, no direct communication with the radius at all. But if we compare the adult wings of the two suborders there can be no question as to the identity of the vein *Rs*, or of its homology in the two groups.

The explanation of this at first rather surprising state of the tracheæ I believe to be that the trachea *Rs* has been detached from the radius and attached to the media. There are everywhere between the principal tracheæ open channels of communication, formed by the

[a] This suture seems to have cut off the subcostal trachea, or else to have dwarfed and diverted its tips. In the cicada the subcostal trachea crosses the nodal suture; and doubtless it once did so in Odonata, for the adult vein extends a little way beyond in three living genera of Æschninæ (compare *Staurophlebia*, Plate XXXIX, fig. 2), and was well developed beyond in the fossil genus *Æschnidium*. The nodus when present in other orders is nearer the wing apex than in the Odonata.

universal anastomoses of the smallest tracheoles. Any one of these

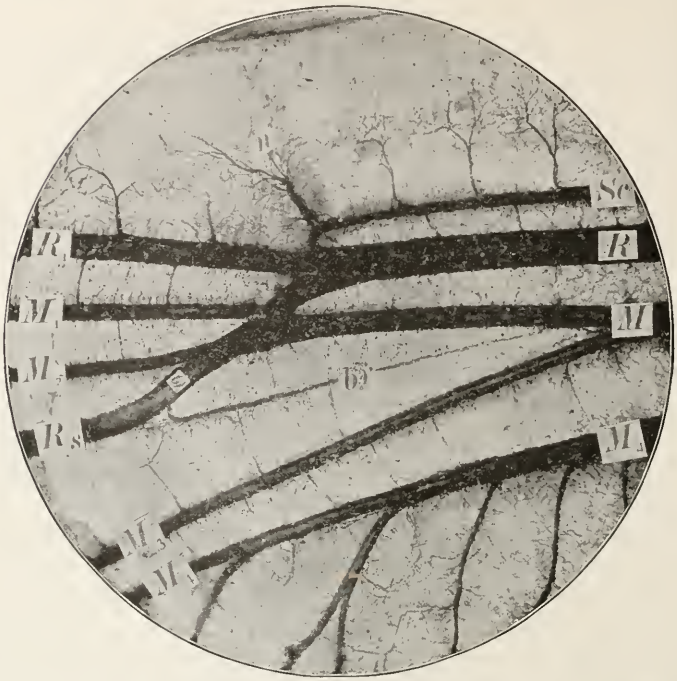


FIG. 5.—TRACHEATION OF THE NODAL REGION OF THE NYMPHAL WING OF *Anax junius* DRURY.

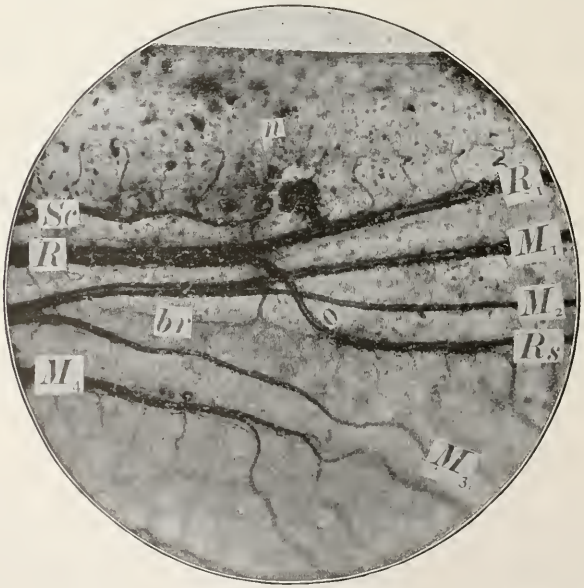


FIG 6.—TRACHEATION OF THE NODAL REGION OF THE NYMPHAL WING OF *Libellula pulchella* DRURY.

open air-passages might become enlarged, should necessity arise for

the entrance of the air from a new quarter. And I think that in this case the necessity may have arisen from the thinning of the wing cases of the slender Zygoptera, whereby the communication of the radial sector with the radius would be gradually pinched off. With the decrease of the air supply from the original source an increased amount must needs come from the medial trunk through tracheoles, some of which would be enlarged and one of which might finally attain the proportions of a tracheal branch, while the base of the radial sector would atrophy.[a]

Either the attachment of the radial sector to media was made at three

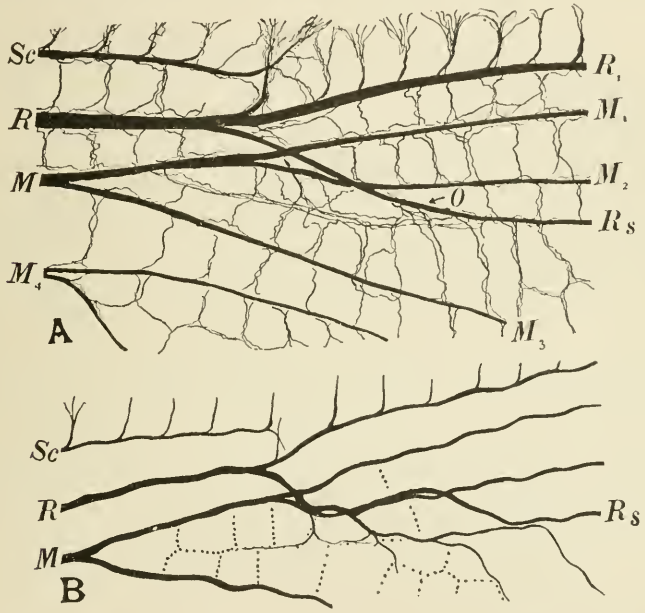


FIG. 7.—TRACHEATION OF THE NODAL REGION OF THE WING. *A*, OF *Didymops transversa* SAY; *B*, OF *Cordulegaster diastatops* SELYS; THE LATTER SHOWING THE MODE OF ORIGIN OF THE TWO OBLIQUE VEINS CHARACTERISTIC OF THE CORDULEGASTERINÆ AND PETALURINÆ.

different places, or else, since its reattachment, it has taken a different course in each of three different series within the suborder Zygoptera. In the Lestinæ we find it separating from vein M_2 far beyond the subnodus, the point of its departure marked by a more or less evident oblique vein, and a long bridge formed about numerous approximated tracheoles, mainly derived from neighboring branches of the media. In the Agrioninæ (*s. str.*) it separates from vein M_{1+2} near the nodus, and there is neither bridge nor oblique vein. In Calopteryx it sepa-

[a] Such shiftings of tracheal branches in insects wings are not unprecedented. Another instance will be cited further on in the case of the branches of the anal trachea. A case of the attachment of trachea M_1 to the radius in *Pieris* has been clearly indicated by Spuler (Zeitschr. f. Wiss. Zool., LIII, 1892, fig. 24, and Enderlein (Zool. Jahrb., Abt. f. Anat., XVI, 1902, pl. III, fig. 20.)

rates from vein M_{1+2} far to the proximal side of the nodus, and about in the more usual position of the proximal end of the bridge.[a]

In this group bridge and oblique vein are lost; but similar parts are found, as will be noted later, extending the attachment of the radial sector to the media still nearer the arculus.

THE REGION OF THE ARCULUS.

Across the base of the wing a strong transverse union of all the principal veins is effected by means of arculus in the middle, triangle at the rear, and antenodal cross veins at the front. Distinct tracheal twigs precede the antenodals of the first (costal) series, while those of the second (subcostal) series are of independent cuticular origin.[b] Specialization is to be traced among these cross veins in their reduction in number and matching in position in the two series, and in the hypertrophy of some of them to form stout triangular trusses, which entirely fill, in section, the furrow between the costa and the radius. Two antenodals, some distance apart, are thus hypertrophied in most Æschnidæ, one at either side of the arculus; in the Thorinæ, but one, and that one meeting the arculus; in *Synthemis* alternate antenodals are thickened, but to a less degree. Their reduction in numbers will be discussed under the general subject of "cross veins."

We have already seen that arculus and triangle are formed where bends in the media and the cubitus, respectively, are met by strong cross-veins. We have seen that the medial and the cubital tracheæ are at first straight or slightly curved as in other insects, and that the bending takes place late in nymphal life, at the time when the veins are forming. The genus *Anax* (Plate XL, fig. 3), while highly specialized in many ways, has preserved a rather primitive condition of the arculus. It is composed here largely of cross vein, which the media bends but slightly to meet, and the veins M_{1-3} and M_4 depart from it in straight lines. Media tends to descend the arculus, and the veins M_{1-3} and M_4, departing from it, become arched strongly toward the radius. In the Libellulidæ the branches of the media become fused at the base while arching upward. This may be traced in the stages attained by such genera as *Neocordulia* (Plate XLII, fig. 1), *Raphismia* (Plate XLIV, fig. 3), and *Pachydiplax* (Plate XLVII, fig. 1). The

[a] Indicating that in this group at least a recurrent tracheole, such as precedes the bridge in the Æschnidæ, may have developed into the basal attachment of the radial sector to the media.

[b] In other orders of insects cross veins are generally wanting from this space, and where present are very few in number.

It will be observed that the tracheal twigs which precede the antenodals of the first series are derived from the subcosta; those of the postnodals of the first series, from the radius. These tracheal branches are clearly the homoiogues of the longer anterior branches of the subcosta and the radius in the Neuroptera and the Orthoptera.

upward arching of the medial branches reaches its climax in some Calopteryginæ, when M_{1+2} after separating from M_3 again rejoins the radius; its basal part then appears as a cross vein, and when its trunk again frees itself it appears as a branch of the radius. *Pseudophaea* (Plate LII, fig. 3), *Calopteryx* (fig. 34), and *Vestalis* (fig. 41) have preserved the steps by which such condition has been attained.

In *Epigomphus* (fig. 8) there is a curious tendency for these medial branches to become conjoined just after their separate departure from the arculus.

In all these tendencies cuticularisation outruns tracheation; the veins become sharply angulated; the tracheæ much less so. This will be clearly seen by comparing nymphal (Plate XXXII, figs. 2 and 3) and adult (Plate XXXV, fig. 3) wings of *Lanthus parvulus*.

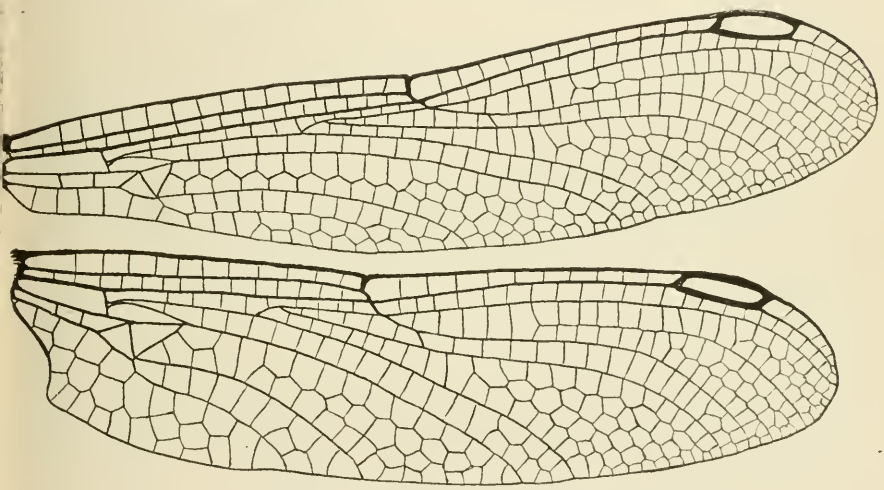


FIG. 8.—WINGS OF EPIGOMPHUS PALUDOSUS SELYS.

The triangle has been called by several writers the "cardinal cell," and worthily, for it is a feature of cardinal importance in the Odonate wing.[a] We have already observed that it is ordinarily formed in *Gomphus* and others of the suborder Anisoptera, between an oblique deflected portion of the cubitus and two cross veins approximated upon the hindmost branch of the media. Between the proximal one of these two cross veins and the arculus is a narrow space which may conveniently be termed the "supertriangle" (*s.*, of all the figures; also called elsewhere "supratriangular space").

The quadrangle of the Zygoptera.—In the suborder Zygoptera triangle and supertriangle bear different relations to each other and to surrounding parts of the wing. Together they constitute a unit of wing structure. They are placed in line, not directed apart by an

[a] It is not always triangular, but the exceptions are few. The name is a very convenient one and in general use, and I use it in a strictly technical sense without regard to shape.

obtruding angle of the cubitus, and are oftenest confluent through the atrophy of the middle cross vein. To the four-sided figure, which together they always present, we will apply the technical term "quadrangle" (*q*, of all the figures; also called elsewhere "quadrilateral, and

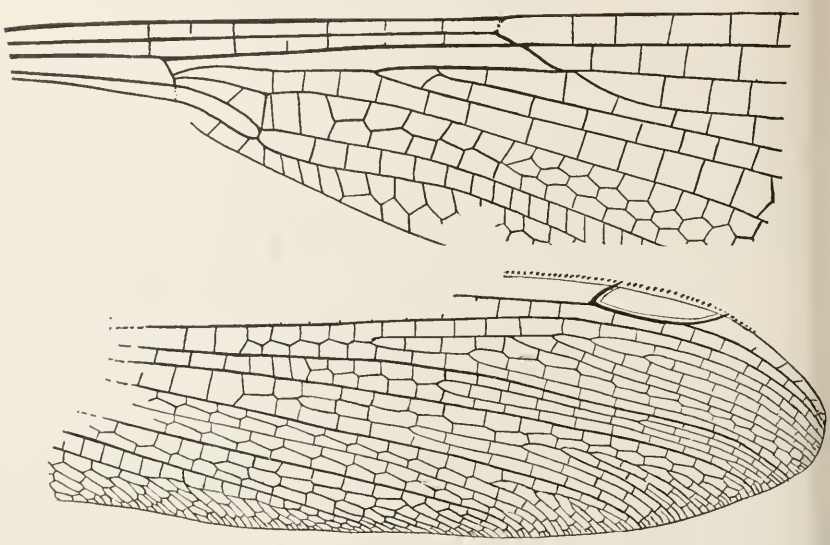


FIG. 9.—WINGS OF A FOSSIL, UNDESCRIBED, AGRIONID GENUS, IN THE MUSEUM OF COMPARATIVE ZOOLOGY.

quadrangular space"). The fossil Agrionid genus illustrated in fig. 9 offers easy transition from the conditions just seen in the Anisoptera to those of the Zygoptera, and renders homologies plain. Comparing this wing with the fore wing of *Tetrathemis* (fig. 10) with respect

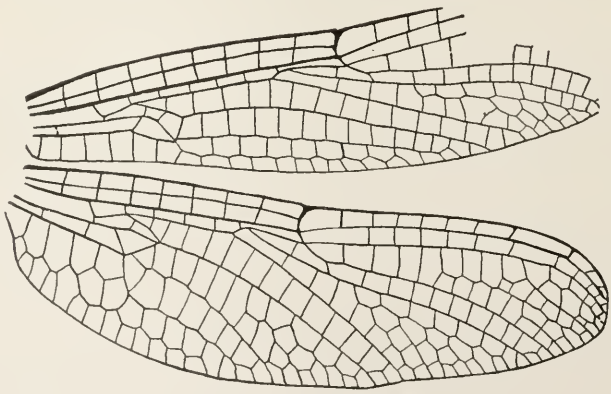


FIG. 10.—WINGS OF *Tetrathemis hyalina* KIRBY.

to the points in question, triangle and supertriangle are recognizable readily in both (though in *Tetrathemis* the latter is elongated and contains an extra cross vein), and both may easily be derived from ordinary rectangular cells.

In Agrionidæ (Plates LIII and LIV) the quadrangle is undivided, the middle cross vein being absent. In the Calopterygidæ (Plate LII) the middle cross vein is occasionally wanting, as in *Anisopleura* and *Epallage*, but in general the quadrangle is elongated and contains numerous extra cross veins, among which the identity of the typical one is lost. The quadrangle is generally rectangular in this family, but in *Hetærina* (Plate LI, fig. 4) it is widened distally and convex anteriorly; in *Thore* (fig. 35) and its allies, exactly the reverse. These facts are illumined when one sees what has been the behavior of the cross vein which terminates the quadrangle in this family. Vein Cu_2, separating from vein Cu_1 at a right angle, and as suddenly bending again distally, sets off a transverse basal portion which is in direct line with this cross vein. The two thus joined rotate together about the hind angle of the triangle as an axial point, while the two forms of quadrangle described above are developing. In *Hetærina* (Plate LI, fig. 4) and *Lais* the medial end of the cross vein has proceeded distally, while the base of Cu_2 has been retracted; in *Thore* (fig. 35), *Rhinocypha*, *Lestes*, etc., the reverse rotation has taken place, as illustrated in the accompanying diagram (fig. 11).

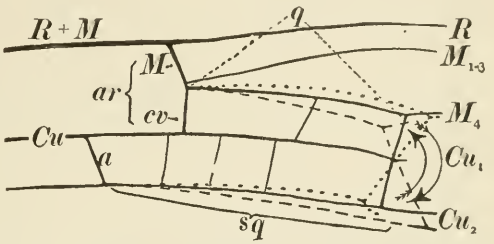


FIG. 11.—DIAGRAM ILLUSTRATING THE BEHAVIOR OF THE QUADRANGLE IN THE CALOPTERYGIDÆ. SOLID LINES, A SOMEWHAT PRIMITIVE QUADRANGLE; LINE OF DOTS, THE QUADRANGLE OF *Hetærina*; LINE OF DASHES, THAT OF RHINOCYPHA; ARROWS INDICATE THE OPPOSITE COURSE OF ROTATION. COMPARE WITH PLATES LI AND LII.

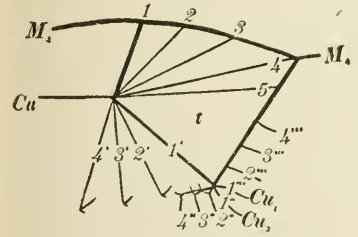


FIG. 12.—DIAGRAM SETTING FORTH THE BEHAVIOR OF THE TRIANGLE IN THE SUB-ORDER ANISOPTERA. THE HEAVY LINES BOUND A SOMEWHAT PRIMITIVE TRIANGLE, 1, 2, 3, 4, AND 5 ARE STAGES IN THE DESCENT OF THE UPPER CROSS VEIN. 1′, 2′, 3′, AND 4′ REPRESENT SUCCESSIVE STAGES IN THE RETRACTION OF THE CUBITUS AT THE TRIANGLE. 1″, 2″, 3″, AND 4″ REPRESENT STAGES IN THE RETRACTION OF THE BASE OF VEIN Cu_2. 1‴, 2‴, 3‴, AND 4‴ REPRESENT STAGES IN THE ASCENT OF THE VEIN Cu_1 UP THE OUTER SIDE OF THE TRIANGLE.

The triangle of the Anisoptera.—Returning now to the suborder Anisoptera, and to the triangle as an individual feature of the wing, we may follow with the aid of fig. 12 the changes that have taken place in it, bringing it from the condition of an ordinary rectangular cell to its present estate. It will be convenient to begin with a triangle hardly more generalized than that of the fore wing of *Tetrathemis*, and to follow the shiftings of its parts severally.

1. The angulation of the cubitus.—At the dividing cross vein of the quadrangle, the cubitus tends in all Anisoptera to form an angle, which pushes triangle and supertriangle out of line, thus destroying the unity of the quadrangle, in making of it two elements of wing

structure. The increasing angulation at this point may be followe in the fore wings of a series of Libelluline genera, such as *Microdipla* (fig. 13), *Anatya* (Plate XLIV, fig. 2), *Mesothemis* (Plate XLV, fig. 3 and *Perithemis* (Plate XLIII, fig. 3). It is only a little less evide in such Gomphine genera as *Agriogomphus* (fig. 27), *Gomphoid* (Plate XXXIII, fig. 2), and *Gomphus* (Plate XXXIII, fig. 1). It wi be observed that this deflection of the cubitus results in the widenin of the space between veins M_4 and Cu_1 beyond the triangle. Th may be seen in the aforementioned genera.

2. The deflection of the middle cross vein of the quadrangle.—It this process that makes the distal half of the quadrangle triangular Successive positions of the cross vein are shown at 1, 2, 3, 4, and 5 c figure. Such genera as *Tetrathemis* (fig. 10), *Anatya* (Plate XLIV fig. 2), *Macrothemis* (Plate XLVI, fig. 1), and *Ephidatia* (Plat XLVII, fig. 2) exhibit these stages. A similar but less striking seri will be seen in such Gomphine genera as *Agriogomphus* (fig. 27

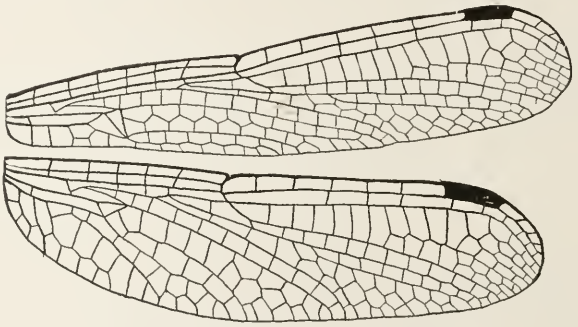


FIG. 13.—WINGS OF MICRODIPLAX DELICATULA SELYS.

Gomphoides (Plate XXXIII, fig. 2), and *Hagenius* (fig. 23). Thi cross vein has become greatly elongated in most Æchnidæ, resultin in the elongation of the whole triangle, as seen in such genera a *Gomphæschna* (Plate XXXVII, fig. 1), *Brachytron* (Plate XXXVIII fig. 2), and *Nasiæschna* (Plate XXXIX, fig. 1). Thus this cross vei has come to lie in such position that it appears in the adult wing t be a continuation of the cubital trunk, and it has generally been s interpreted.[a]

[a] *Pentathemis membranulata* Karsch (Ent. Nachr., XVI, 1890, pp. 33–35) presents somewhat unusual condition of this cross vein, in that it is declined to the maximu and bent upward in the middle at its junction with a cross vein in the supertriangl which has migrated outward upon it half the length of the triangle. This condition very like that seen in the hind wing of Tetrathemis (fig. 10), only a little i advance of that, has resulted in the triangle, after once attaining triangular form becoming again four sided. Clearly, it is not five sided as Karsch thought. Hi alternative explanation (same reference, p. 35), rejected because the triangle woul not reach vein M_4 and the supratriangle would be in contact with the discoida areolets—a condition seen in the hind wing of *Necordulia* and *Hemicordulia* (Plat XLII, figs. 1 and 3) and in many Libellulinæ—is the right explanation, and th name *Pentathemis* is the result of a misinterpretation.

3. The ascent of vein Cu_1.—The cubital fork is in all Odonata at the ıind angle of the triangle. When the distal end of the anal vein ıeets the cubitus squarely at this point, a struggle ensues between he branches of the cubitus for the maintenance of this strong point of support. In a series of genera Cu_2 wins, and Cu_1 is starved and rowded out, becomes much the weaker vein, and is forced to ascend he outer side of the triangle. This has happened in both fore and ıind wings of *Pseudophlebia minima* (Plate XLV, fig. 1). The sucessive positions it assumes are epitomized in the diagram; they may e verified in the hind wings of such genera as *Agrionoptera* (Plate XLIV, fig. 1), *Mesothemis* (Plate XLV, fig. 3), *Diplacodes* (Plate XLV, ig. 2), and *Microdiplax* (fig. 13).

4. The descent of vein Cu_2.—A happier solution of the struggle just ıentioned is found when vein Cu_1 is left in possession of the hind ıngle of the triangle, vein Cu_2 descending at a right angle from the fork, carrying the tip of vein A_1 with it for its own support. We have already seen that a very perfect adjustment of this sort exists throughout the Caloptery-gidæ, where vein Cu_2 appears as the direct continuation of vein A_1. Our diagram illustrates the manner in which this adjustment is brought about in the Libellulidæ. This will be better understood by examining the fore wings of such genera as *Agrionoptera* (Plate XLIV, fig. 1), *Anatya* (Plate XLIV, fig. 2), *Raphismia* (Plate XLIV, fig. 3), and *Ephidatia* (Plate XLVII, fig. 2).

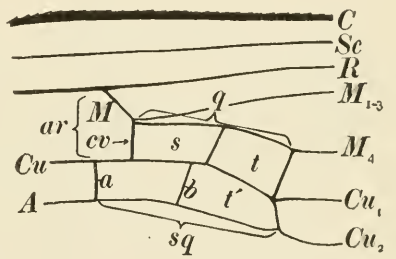


FIG. 14.—DIAGRAM SHOWING BASE OF TYPICAL DRAGON-FLY WING; SHOWING AT *a* AND *b* FIRST AND SECOND CUBITO-ANAL CROSSVEINS; SHOWING ALSO QUADRANGLE (*q*), SUBQUADRANGLE (*sq*), SUPER-TRIANGLE (*s*), TRIANGLE (*t*), AND SUBTRIANGLE (*t'*).

Differentiation between fore and hind wings at the triangle.—Primitively, fore and hind wings of Odonata were alike, and the arculus was a little beyond the triangle in both, with the anal vein extending to the hind angle of the triangle (conditions still preserved in *Cordulegaster* (fig. 25)). The above diagram of these parts (fig. 14) will therefore stand for either wing.

In the space between the cubital and anal veins before the triangle are two crossveins which may fairly be considered typical, and which, because of the frequent necessity for reference to them, we will designate as the first and second cubito-anal crossveins (*a* and *b* of all the figures). The part of the cubital space beyond the first cubito-anal crossvein will be seen to lie directly beneath the quadrangle (which it much resembles). It may be conveniently designated as the "subquadrangle" (*sq*), and the part of this beyond the second cubito-anal crossvein as the subtriangle (*t'* of all the figures; called also, elsewhere, "subtriangular space" and "internal triangle").

Differentiation between fore and hind wings has been most com pletely carried out in the Libellulidæ,[a] and, fortunately, almost all th steps are still to be seen in living genera. In this family two ver different processes have operated in the two wings:

1. *The procession of the triangle in the fore wing.*—In all but th more generalized Libellulidæ the anal vein seems to run directly t the antero-internal angle of the triangle, while retaining in the hin wing its usual course to the hind angle. This is a puzzle; but the ke to the puzzle is found in the behavior of the second cubito-anal cross vein and the anal vein. The accompanying diagram (fig. 15) epitc mizes what has taken place.

The anal vein formerly went directly to the hind angle of th triangle in the fore wing. Then, through the simultaneous deflectio of crossvein and anal vein, the latter came to appear forked—a stag it has reached and still mair tains in most Gomphina Then the basal part of th anal trunk was carried for ward into direct line wit the still further deflecte second cubito-anal cross veins, so that the latter ap pears as the continuation c the vein, and not at all as crossvein, while the dista end of the anal vein is almos lost among the crossveins o the proximal side of the tr angle. Thus it is that th anal vein seems to join th front angle of the triangl

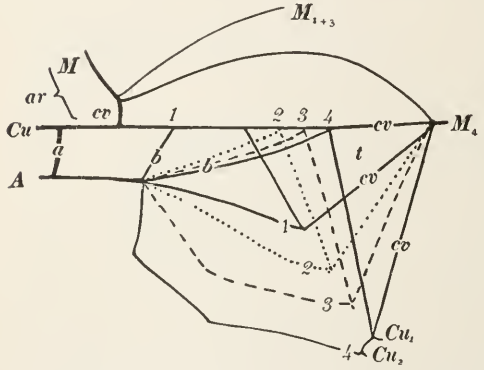


FIG. 15.—DIAGRAM ILLUSTRATING THE PROCESSION OF THE TRIANGLE AND THE DEFLECTION OF THE ANAL VEIN AND SECOND CUBITO-ANAL CROSSVEIN IN THE FORE WINGS OF LIBELLULIDÆ. *a*, THE FIRST, AND *b*, THE SECOND CUBITO-ANAL CROSSVEINS; 1, 2, 3, AND 4, SUCCESSIVE POSITIONS.

With the acquisition of new responsibilities, the second cubito-ana crossvein has waxed stronger and longer, and has pushed the inn angle of the triangle toward the outer, making the triangle narrow and bringing about by this means its apparent remoteness from th arculus. Such genera are illustrated in Plates XLIII, XLV, an XLIX, and show the steps in this process. Simultaneously th

[a] Their differentiation in function was proved experimentally by Girard (186 Note sur divers experiences relatives a la fonction des ailes chez les insectes, An Soc. Ent. France, (4), II, pp. 153–162). His results that are of most interest he were gotten by simply clipping off one pair of wings at a time. Thus he showed th in *Agrion*, with fore and hind wings practically alike, flight is fairly well sustain with either pair of wings alone: Libellula can fly with the fore wings only, but wi the fore wings removed the hind wings alone will not sustain it in the air. I ha verified these results, using *Enallagma* and *Sympetrum*. I have also made some ne experiments to determine the utility of certain structures. Brief reference will b made to my results farther on.

deflected portion of the cubitus (the inner side of the triangle) has been elongated, producing the very narrowly elongate triangle of *Libellula* (Plate XLVIII, fig. 3) and its allies.

B. The recession of the triangle in the hind wing.—The behavior of the triangle in the hind wing has consisted simply in its retraction through the successive position shown diagrammatically in fig. 16, and illustrated in such genera as *Agrionoptera* (Plate XLIV, fig 1), *Raphismia* (Plate XLIV, fig. 3), *Uracis*, (Plate L, fig. 2), and *Pantala* (Plate L, fig. 3). Doubtless this recession of the triangle of the hind wing could only be advantageous in connection with the developments described under the next heading and discussed again farther on.

The anal area.—In the Odonata there is no anal furrow or suture, as in most other insects, sharply delimiting an anal field. The anal vein, except in a few fossil forms (*Isophlebia*, fig. 31, etc.), is solidly joined to the cubitus, as already shown. We now pass to notice the distribution of the anal branches in the small area back of the cubital deflection.

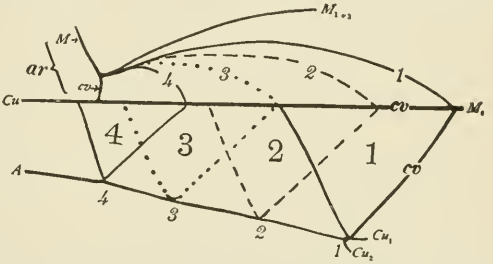


FIG. 16.—DIAGRAM REPRESENTING THE RECESSION OF THE TRIANGLE IN THE HIND WINGS OF THE LIBELLULIDÆ, 1, 2, 3, AND 4, SUCCESSIVE STAGES.

Probably in the early Odonata the anal tracheal trunk occupied the position of the anal vein, well back of the cubitus. Ontogeny (see figs. 1 and 2) and analogy with insects of other orders would both support this view. But in such recent forms as I have had for study this anal trachea is closely approximated to the cubitus beyond the base, and, midway to the triangle, descends to the level of the anal vein, and sends branches both proximally and distally, about which that vein is formed (fig. 2, and Plate XXXI, figs. 1–3). Even in the thick wings of nymphs of Anisoptera the contorted position and decreasing size of the anal trachea indicate that, like the costal trachea of the opposite wing margin, it is suffering from lack of room; or, perhaps, outstripped by the intervening tracheæ that are better situated in relation to air supply. At least we find, especially in thin and narrow wing cases, the anal trachea dwindles, and loses successively all its branches, which then become incorporated into the cubital air system. The best developed anal trachea we have seen is that of *Anax* (Plate XXXI, fig. 3), in which it will be noticed that the terminal branch, A_1, is continued beyond its position of fusion with the cubitus in a recurrent position. In the hind wing of *Gomphus* (Plate XXXI, fig. 1) it will be observed that this recurrent portion is attached to vein Cu_2; A_1, apparently, wanting; A_2, strongly developed. In the fore wing of the same nymph A_2 has also been transferred to the cubitus, being

attached to the cubital trunk at the place where the anal vein bends strongly away from it. In all the Zygoptera I have been able to examine, all the branches of the anal vein have been transferred to the cubitus in both wings, the anal trunk being very greatly reduced or wanting (see Plate XXXI, fig. 2).

Such transference of the branches of the anal trachea lends the strongest support to the assumption already made regarding the transference of the trachea *Rs* to the media, in which case possible reasons for shifting and reattachment were much more clear.

The anal loop.—Owing to such shiftings of trachea, owing also to the expansion of this region in some wings, occasioning the development of accessory tracheal branches and its reduction in others, causing all the branches to disappear, the homologies of those branches which are oftenest present are followed with difficulty. Two of them, however (designated as A_1 and A_2 in the figures), must be considered here, since they together form an inclosure, which becomes one of the strongest

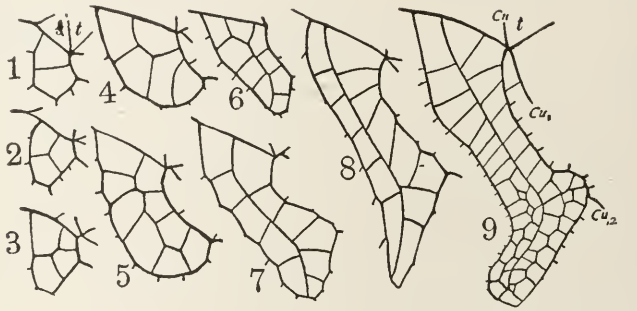


FIG. 17.—FORMS OF THE ANAL LOOP IN THE ANISOPTERA: 1, ANAL LOOP OF CYCLOPHYLLA DIPHYLLA; 2, OF *Gomphoides stigmatus;* 3, OF *Gomphæschna furcillata;* 4, OF *Gomphomacromia paradoxa;* 5, OF *Syncordulia gracilis;* 6, OF *Agrionoptera insignis;* 7, OF (?) *Nannophya maculosa;* 8, OF *Ephidatia longipes;* 9, OF *Hydrobasileus extrancus.*

of the supporting structures of the expanded anal area of the hind wings of the Anisoptera. This inclosure may fitly be designated as the *anal loop* (*al.* of all the figures). Fig. 17 will serve to show some of its more common and characteristic forms.

In some Aeschnine genera we find a supplemental loop (*al'*) developed between veins A_1 and Cu_{2a}. Fig. 3 of Plate XXXI shows how this is brought about; it is another accompaniment of the widening of the base of the wing. Since in the Libellulidæ the anal loop extends from vein A_2 to vein Cu_{2a}, it is to be considered as the equivalent of both loops in *Anax*. Of the characteristic foot-shaped loop of the commonest Libellulidæ the "toe" is of later development, and results from the concurrent elongation of veins A_2 and Cu_{2a} with the expansion of the hind angle of the wing.

After considering these changes severally, if we again compare fore and hind wing in any of the more specialized Libellulidæ we shall see

that only the part of the wing which lies back of the median vein has been affected by them. But that part has been modified profoundly; in it entirely different ends have been wrought out in the two wings, and by different means. The fore wing is characterized by greater modification of parts present in the primitive wing; the hind wing, by the greater development of new parts.

III. SOME GENERAL FEATURES OF THE WING.

VEIN SHIFTING AND VEIN DIFFERENTIATION.

There are two kinds of specialization occurring simultaneously in insect wings, not clearly delimited, but, nevertheless, distinct enough to enable us to understand in a measure the reasons for the success of both. First, there is the shifting of veins for the mechanical advantage of position and the development of strong cross veins to aid in maintaining favorable positions. These developments have occupied our discussion hitherto. We have seen that the course of specialization is traceable in each part, and we shall see further on that the parts, varying independently or being modified together, collectively furnish most excellent characters for interpreting the genealogy of the group.

Second, there is a specialization which is not confined to any particular part of the wing or to any particular structure, but which consists in the progressive differentiation between veins and membrane, in the concentration of strength-giving wing material within the supporting veins, and in the reduction of cross veins. Although less tangible, perhaps, and certainly less useful for tracing genealogies, this kind of specialization is none the less real. The first furnishes characters differing in kind; the second, only those differing in degree. The first, rather than the second, is characteristic of fossil species, some fossil forms having carried the shifting of veins already described to extremes unparalled at the present time. The second, rather than the first, is characteristic of those modern genera which belong to the cooler regions of the globe. The first is often accompanied by very abundant[a] venation. The second is indicative of keener competition in recent times and in temperate climates, necessitating greater economy of wing-building substance.

A comparison of the wings of *Neurothemis* (fig. 18) and *Tetragoneuria* (fig. 19), two genera of Libellulidæ that may fairly be taken as exponents of the two kinds of specialization, will make the difference between them clear. In *Neurothemis* we have venation "run wild"—the vein-building material scattered with great prodigality throughout the membrane, forming a very irregular and inconstant mesh work,

[a] One might almost say luxuriant. Possibly the advantage of the new position attained by the shifting of parts is so great that over development results from it at first.

such as was common to many early fossils of other orders and such as is still characteristic of the tegmina of the Locustidæ. In *Tetragoneuria*

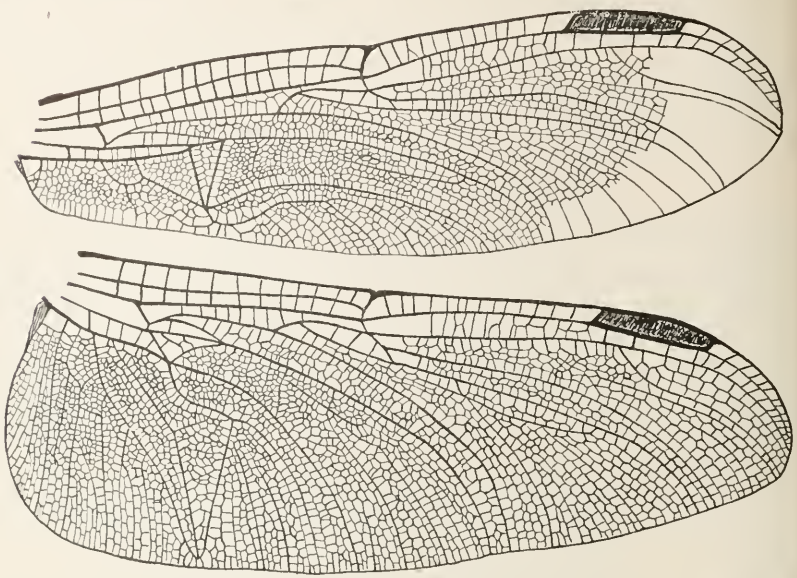


FIG. 18.—WINGS OF *Neurothemis oculata* FABRICIUS.

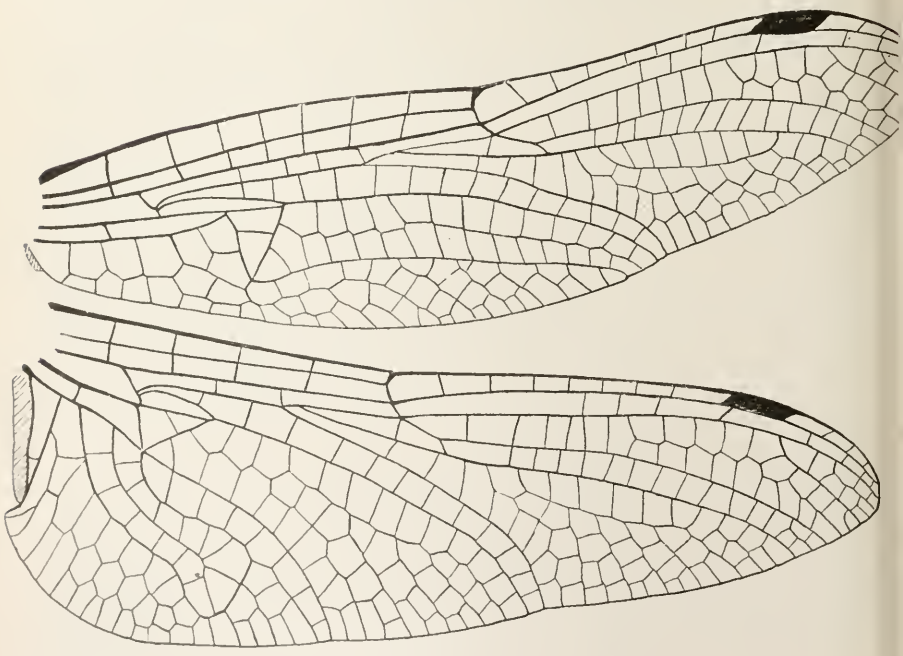


FIG. 19.—WINGS OF *Tetragoneuria cynosura* SAY.

order is wrought out of this seeming confusion in the wing membrane. The veins are strong, the membrane is thin and more transparent,

cross veins are reduced so as to leave those that remain in such position that each seems to bear its individual share in the stress upon the wing. Instead of a dozen, more or less, of inconstant cross veins in the space between veins R_1 and M_1 between nodus and stigma, as in *Neurothemis*, there are but three, and these three are constant, and so for other parts. In and about the triangle of *Neurothemis* are many veinlets which have been sacrificed to make the triangle itself stronger in *Tetragoneuria*. An actual count of the cells in a hind wing of *Neurothemis* gives the number 2,695; in a hind wing of *Tetragoneuria*, 265, the latter wing being at the same time a little larger. *Neurothemis* has far outrun *Tetragoneuria* in all those adjustments of parts in the region of the areulus, already described, as characteristic of the specialization of the Libellulidæ; but *Tetragoneuria*, having attained a fair measure of mechanically advantageous arrangement of parts, has attained success by disposing of its strength-giving wing material where it is most effective. *Tetragoneuria* is vastly superior in flight[a]—is, indeed, one of the fleetest and most agile of winged creatures.

CROSS VEINS.

The vein-building substance of which we speak is of course hypodermis. The insect wing is essentially but a flat evagination of the body wall, with a few trachea grown out into it. During early development the hypodermis of the wing does not differ in any essential respect from that of other parts of the body. As elsewhere, it consists of a single layer of cells which secrete a protecting external layer of chitine. At the time of transformation, when the hypodermis of the two walls of the wing sac is bound together by fused internal processes, blood is forced out into the wing, greatly extending it laterally. The hypodermis is thus spread out in a very thin layer. As soon as a definitive layer of chitine is deposited, the hypodermal cells (which, of all cells known to me, possess the greatest capacity for speedy and extensive shifting and readjustment) begin to be segregated into groups along the lines of the veins that are to be, and there deposit additional chitine, which differentiates veins from membrane.

Doubtless in the earliest insect wings the segregation of the hypodermal cells was such as to give a membrane crowded with somewhat circular areoles, such as we find in the expanded lateral margins of the pronotum of the Tingitidæ, in the tegmina of the Locustidæ, in almost the entire wing of the fossil dragon fly *Eschnidium*, and in the wider spaces of the wing of *Neurothemis*. The principal veins first would become strongly marked by the accumulation of the hypodermal cells about the tracheæ. Cross veins would emerge from the meshwork, as they seem to be emerging in the wing of *Neurothemis*, in the spaces between veins R_1 and M_1, between M_3 and M_4, etc., by the dropping

[a] I venture this unqualified statement without having seen *Neurothemis* fly.

out of veinlets that are longitudinally placed; or, as illustrated in the following diagram (fig. 20).

A few strong cross veins for binding the longitudinal veins together would be developed first. In the wider spaces between the longitudinal veins the cells would take on hexagonal form as soon as necessity for economy in the disposition of vein-forming substance arose, and hexagons would, of necessity, fall into regular series or rows. This condition would early be attained—has been attained or surpassed by almost all living Odonata. Meanwhile the reduction among cross veins goes on apace, and the fundamental thing in this reduction consists in the better marshaling of the hypodermal cells at the proper moment of transformation.

This brings us to the practical point, that cross veins are constant in number and position only when they have attained individual responsibility—when each has its own share in the stress of the wing stroke. Utility determines survival among cross veins as among species. No better illustration could be found than the two cubito-anal cross veins before the triangle in the wings of the Libellulidæ. The first of these is formed, as we have seen, about the descending portion of the anal

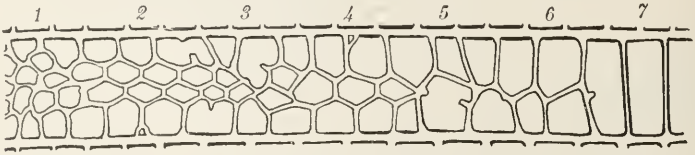


FIG. 20.—DIAGRAM ILLUSTRATING THE EMERGENCE OF STRONG CROSS VEINS.

trachea, and that is a sufficient reason why in the reduction of cross veins it never disappears. The second in the fore wing becomes braced against the front angle of the triangle and acquires new responsibility, which insures its preservation; one would as soon expect to miss those other cross veins which bound the triangle. But in the hind wing this same cross vein acquires no such importance—rather loses through the recession of the triangle any importance it may have had to begin with, so it early disappears. In the more generalized Libellulidæ it is always present; in the more specialized it is uniformly absent, but in a few, in this respect transitional genera, it is present or absent indifferently. Similarly in the more specialized Libellulidæ but one cross vein persists in the space which the bridge incloses, and there is a very good reason why that one never disappears—it is formed about the descending trachea which precedes the bridge.

Very similar are the antenodal and postnodal cross veins, of which so much use has been made in systematic work. In the fore wing of *Neuraeschna* the antenodals are more than forty, the number being inconstant; in *Pachydiplax* they are always six. In the hind wing of *Neuraeschna* the antenodals are about twenty-five; in that of *Tetra-*

goneuria they are four. Those antenodals which early chance become "matched" across both costal and subcostal spaces brace the deepening subcostal furrow better and are more sure to be preserved.

Then there is a reduction of cross veins which seems not solely directed toward strengthening those that remain, but rather toward clearing out of spaces between the points of transverse union of longitudinal veins.[a] This clearance takes place in different places in Libellulidæ and in Gomphinæ, correlated with the difference in shape and position of the triangle in the two groups. In the former the cross veins disappear (see *Pachydiplax*, Plate XLVII, fig. 1) from the spaces adjacent to the subnodus and the oblique vein and under the stigma. In the latter (see *Gomphus dilatatus*, Plate XXXIII, fig. 1) from the spaces just beyond the arculus. In the Æschninæ, with triangles similarly disposed, while the cross veins do not actually disappear just beyond the arculus, we find sometimes (as in *Anax*, Plate XL, fig. 3)

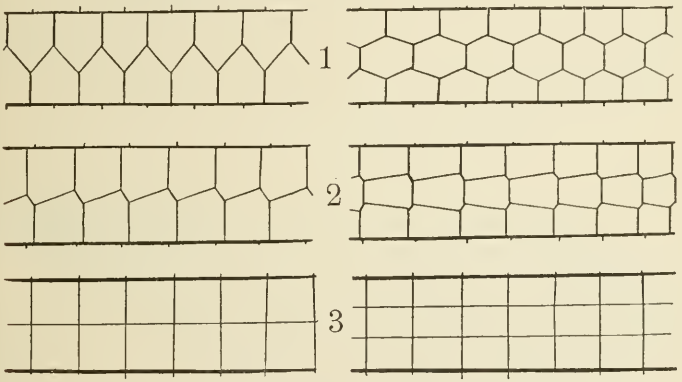


FIG. 21.—DIAGRAM SHOWING HOW HEXAGONAL CELLS BECOME RECTANGLES AND HOW CROSSVEINS BECOME MATCHED IN TRANSVERSE LINES ACROSS THE WING.

all the veins on the anterior side of the base of vein M_4, between it and the radius, so dwindled that little more than thin membrane remains. This is much more evident in the actual wing than in the figure.

We have already referred to the matching of nodal crossveins. In the Agrioninæ this process is carried so far that all the crossveins of the body of the wing become arranged in transverse lines. A comparison of the wings of *Archilestes* (Plate LI, fig. 6), *Lestes* (Plate LIII, fig. 1), *Argia* (Plate LIII, fig. 5), and *Nehallennia* (Plate LIV, fig. 8) will illustrate the progress of this tendency.

[a] Allowing, perhaps, for readier flexion of the portion of the wing posterior to the cleared spaces, though of this I am not sure. In Myrmeleonidæ (Plate XXXVI fig. 2) subcosta and radius are strongly bound together at base and at stigma, while the long narrow space between is free from cross veins. It would seem, since the wing is easily flexed behind this space, the costal margin remaining rigid, that an imaginary axis of flexion joins the two strong yet elastic terminal points of union.

The accompanying diagram (fig. 21) shows the steps by which crossveins may be brought into line. All these steps may be seen in the wings of Agrioninæ represented in the plates and better still in fig. 9.

In Calopterygidæ crossveins are so numerous it seems to have been of more moment (at least in Calopteryx and its nearest allies) that the longitudinal lines of crossveins should become straight, allowing the longitudinal furrowing of the base of the wing to be extended to the margin.

SECTORS AND SUPPLEMENTS.

The areolæ, or cells, of the wing membrane are potential hexagons. Where bordered on one side by a straight vein they are converted into pentagons by the elimination of one angle; where included in a single row between two veins they become quadrilaterals, through the elimination of two angles. Even in the broader areas of the wing their hexagonal regularity is early disturbed by two more or less distinct means: (1) by the development of new tracheal branches, which penetrate into the broader spaces, straightening out certain broken lines of crossveins and converting their bordering hexagons into pentagons; (2) by the development of longitudinal veins, independently of the tracheæ—veins which traverse the same spaces in a direction generally more or less transverse to that of the accessory tracheæ and complete the havoc of the hexagons. By the first means are produced extra branches of principal veins, which so appear in the adult wing. Some of the most important of these are designated M_{1a}, Rs_a, Cu_{2a}, etc., in the figures. By the second means are developed curved veins, which are generally opposed in position to the principal veins bounding the wider spaces anteriorly. These may be called *supplements*. Both are well shown, and the difference between them is clearly demonstrated by Plate XXXII, fig. 1 of *Anax junius*. The principal trachea shown is the radial sector, whose branches are accessory; the strong, developing vein that sets across them, bending toward the radial sector at both its ends, is the *radial supplement* (*R. suppl.*, of all the figures). It will be seen to be a purely cuticular vein, without trachea of its own. Behind vein M_1 is an exactly similar vein, the median supplement (*M. suppl.*, of all the figures). Behind vein M_1 and proximal to vein M_{1a}, though often joined to the latter, is another, the apical supplement (*ap. suppl.*), well shown in *Tramea* (Plate XLIX, fig. 3) and its allies. From the outer side of the triangle there starts another, the trigonal supplement (*trig. suppl.*) well shown in *Hagenius* (fig. 23), and in most Æschninæ (Plates XXXVII–XL).

Both supplements and extra branches, being relatively recent acquirements, are well developed only in the more specialized members of the several groups.

UNEQUALLY DEVELOPED WINGS IN THE SAME SPECIES.

1. *The specialization of fore and hind wings to an unequal degree, when both (or the parts concerned of both) are following similar lines.*—A single illustration of this will suffice. In *Chalcopteryx* (fig. 22) the fore wing has in several points outrun the hind. For instance, vein M_2 separates from vein M_1 in the hind wing at the subnodus, as is usual; but in the fore wing M_2 has fused with M_1 for the space of several cells' length beyond the subnodus. Again, in the space between veins M_1 and M_2 there are a number of interpolated sectors, all of which are independent of the veins in the hind wing, but in the fore wing the next to the longest of these has become attached to vein M_2 in such position that M_2 now appears forked. It will be seen at a

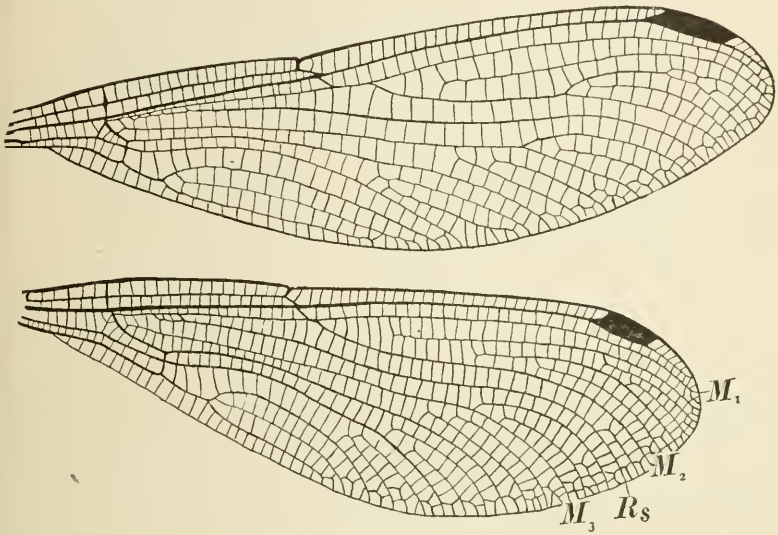


FIG. 22.—WINGS OF *Chalcopteryx rutilans* RAMBUR.

glance that the anterior branch of this fork is the same thing as the independent sector occupying the same position and relations in the hind wing. First, a broken line of crossveins became straightened out longitudinally to form the sector; then, one of the crossveins lying below its proximal end in the fore wing became declined to brace the sector against vein M_2. But the bracing of the wing tip did not stop with this. The upper branch of the fork has acquired a lesser fork of its own, whose anterior branch is in like manner developed out of a still shorter sector, which has remained independent in the hind wing. Again, the longer of the two sectors in the space between veins Rs and M_3 in both wings become attached to vein M_3; a symmetrical fork has thus been developed in the fore wing, but in the hind wing the adjustment is still imperfect.

2. *Unequally developed wings in the two sexes.*—The wings of the male often outrun those of the female. The best-known instance is the frequent angulation of the anal area of the hind wing in the male, the hind angle of the female always remaining rounded. In *Hagenius* (fig. 23) it will be seen that the difference in conformation of the anal angle has slightly affected the form of the anal loop also.

In that part of the Calopterygine series in which the stigma is lost it is retained longest in the females.

In *Agrion* (fig. 4, *t.*) it retains a much more primitive form in the female. The curious stigma of the fore wing of the male of *Anomalagrion* (fig. 4, *a.*) has outstripped that of the hind wing, but even the latter is somewhat less primitive than either stigma in the female.

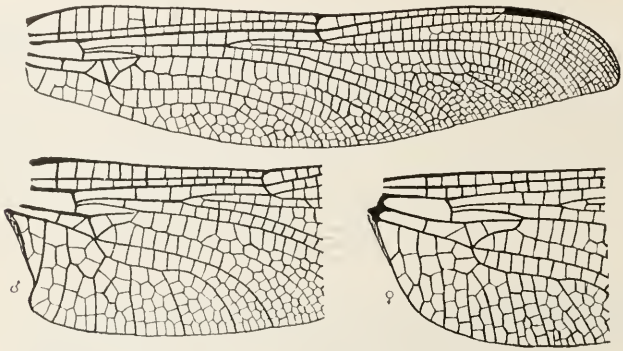


FIG. 23.—WINGS OF *Hagenius brevistylus* SELYS.

The reason for the greater specialization of the wings in the male is, of course, so well known as to need only passing mention. The males, and not the females, seek their mates and compete for them upon the wing, often amid great rivalry.

SUMMARY OF THE MORE GENERAL TENDENCIES OF VEIN EVOLUTION WITHIN THE ORDER.

The facts of ontogeny and comparative anatomy hitherto presented seem to warrant a number of conclusions as to the development of the several parts, which conclusions may be expressed in tabular form as follows:

Generalized condition.	*Developmental tendencies.*
Subcosta long; nodus remote from wing base.	Subcosta becoming shortened and the nodus retracted.
Antenodal and postnodal cross veins numerous, weak, irregular (not matched), and none of them hypertrophied.	Antenodal and postnodal cross veins becoming reduced in number, stronger, more regular, sometimes matched in position or differentiated among themselves.
Stigma without special support.	Stigma becoming supported, proximally by a brace vein (hypertrophied cross vein), and distally by a sector (M_{1a}).

Bridge weakly or incompletely developed; oblique vein remote from the subnodus.	Bridge becoming strong and directly attached to vein M_{1+2}; oblique vein, retracted toward the subnodus.
All principal veins straight or gently curved and evenly forking.	Some principal veins becoming strongly angulate at points of special bracing.
Media at the top of the arculus.	Media descending the arculus.
Veins M_{1-3} and M_4 at their departure from the arculus, separate and straight.	Veins M_{1-3} and M_4 becoming fused, or strongly arched upward, or both.
Triangle, supertriangle, subtriangle, etc., ordinary quadrangular areoles (perhaps traversed by weak cross veins).	Triangle, etc., becoming strong and highly differentiated inclosures.
Cubitus somewhat symmetrically forked.	Cubital fork becoming strongly unilateral.
Anal angle of the wing unsupported.	Anal angle becoming supported by the junction of veins Cu_2 and A_1 and, sometimes, by the development of an anal loop.
Cross venation dense, irregular, and inconstant.	Cross veins becoming fewer, stronger, more definite and regular, and the membrane, thinner.
Fore and hind wings alike.	Fore and hind wings differentiating (1) by following parallel paths with unequal speed, and (2) by following different paths.

IV. LINES OF SPECIALIZATION.

Hitherto we have been discussing wing characters more as individual entities than as mutually dependent parts of a single organ. The illustrations of the steps in the development of each, drawn from adult wings, have been selected arbitrarily, and have not always been drawn from a single line of development. They have served the purpose of illustrating in a general way the progressive modifications of each part, confirming the ontogenetic record. In their application to this end we have necessarily overlooked the lesser individual peculiarities of each. Correlated characters varying independently preserve, some here, some there, bits of the ancestral record, but with more or less of individual alteration of it. It is probable that every one of the characters discussed in this paper would be found on closer study to possess distinctive features in each genus—earmarks of the genus. This, of course, applies not to wing parts alone, but to every other part as well.

We come now to consider these same characters in their ensemble. Their individual records, of course, do not agree. Did they agree, we should have a single lineal series, very well adapted to book making. We should have a wing exhibiting the generalized characters just mentioned with which to begin the series. But while it has been easy to show by concurrent ontogeny and comparative morphology that

the characters there presented are relatively primitive for the group, and while each of these characters is exhibited in some of the more generalized forms, it is quite impossible to find a single wing embodying them all. Let us therefore now carefully compare the several records and discover, if we may, the history of the principal Odonate wing types.

THE FIRST DICHOTOMY.

The first dichotomy has been already indicated, or, at least, implied. Aside from the crossing of the radial sector, respecting which all dragon-fly wings are in essential agreement, the quadrangle has certainly played the most important rôle in the evolution of these wings. Upon the quadrangle two distinct tendencies have operated, producing the suborders Zygoptera and Anisoptera. In the former the tendency has been to preserve the quadrangle as a unit of wing structure, to continue vein Cu_1 outward from it in direct line, and to set off Cu_2 squarely upon the distal end of vein A_1. In the latter the tendency has been to divide the quadrangle into triangle and supertriangle, and to differentiate between fore and hind wing. Supplements are developed only in the latter, while the tendency toward the matching of cross veins and the reduction of the base of the wing are characteristic only of the former.

SUBORDER ANISOPTERA.

Again, in the two great families of this suborder two dominant tendencies are almost equally plain. In the Æschnidæ these are toward (1) the similar elongation of the triangle in both wings; (2) the development of strong supplements; (3) the hypertrophy of two antenodal cross veins; (4) the development of a brace to the stigma, and (5) the angulation of the hind angle of the hind wing in the males. In the Libellulidæ there is the single, more definite, and more exclusive tendency, already discussed, toward the differentiation between fore and hind wings at the triangle.

A. Æschnidæ.—The family Æschnidæ is a bundle of remnants. In it are found no less than eight fairly distinct types of venation. The types represented by *Heterophlebia*, *Stenophlebia*, and *Æschnidium*[a] are extinct. That of *Petalura* was much more abundant in past times than now. *Chlorogomphus* and *Cordulegaster* are represented by but a few isolated species. Only the groups of *Gomphus* and *Æschna* are dominant at the present time. In some cases, therefore, there is no

[a] Attention should be called here to the peculiar and altogether isolated type of venation found in *Æschnidium*. In wings, otherwise like those of the Æschnidæ, the shifting of the anal vein up toward the inner angle of the triangle is completely carried out in both fore and hind wings. In this, and also in the secondary developments for supporting the expanding anal angle, *Æschnidium* far outran all living forms. In the matter of differentiation between veins and membrane, however, and the reduction of cross veins, it remained very generalized indeed.

terial to be had for tracing genealogies, and we will attempt to point out only the more important venational features, comparing them with the conditions we believe to be primitive for the order.

Chlorogomphus.—This (fig. 24) is an isolated living type, specialized in the extensive differentiation between fore and hind wing by the development of an expanded anal area upon the latter, generalized in its unbraced stigma and in its retention of cross veins in the space before the arculus. It parallels *Macromia moorei* in the peculiar form of its anal loop, and *Hemianax ephippiger* (Plate XXXVI, fig. 3) in the circuitous course of vein Cu_2. It is unique among the Odonata known to me in that the triangle of the hind wing has been elongated transversely to the axis of the wing, while that of the fore wing is equilateral.

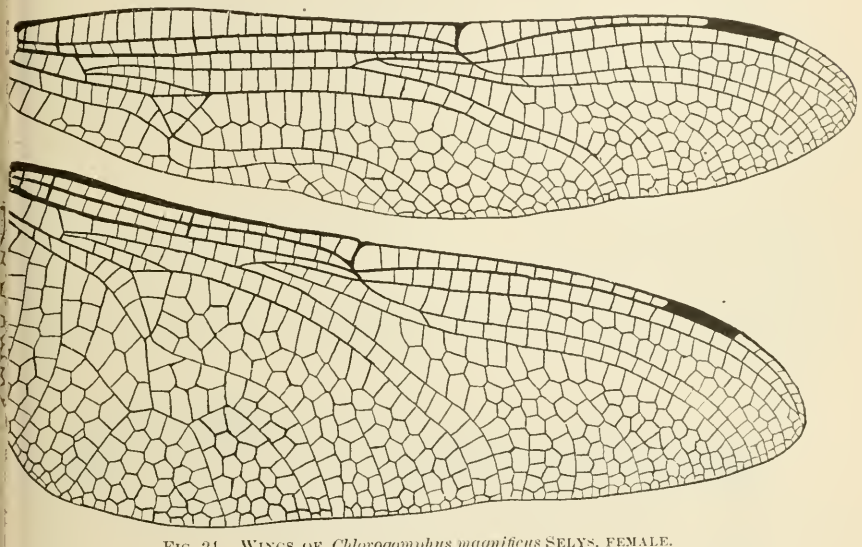


FIG. 24.—WINGS OF *Chlorogomphus magnificus* SELYS, FEMALE.

The Cordulegaster group.—This small group has retained some decidedly primitive features. Anal vein and second cubito-anal cross vein have retained their primitive position and relations in both wings. The triangles are alike, and only moderately elongated. No supplements are developed; and there is no brace to the stigma, or only a very imperfect one in *Petalia* and its allies. There is, however, a moderate enlargement of the base of the hind wing, and this becomes angulate in the males. *Cordulegaster sayi* (fig. 25) and *Phyllopetalia apicalis* (fig. 26) represent the divergence of the group; there is uniformity in the more important wing characters. There has been a slight development of accessory branches upon the radial sector, and in the wing of *Phyllopetalia* will be noticed the undulate course taken on by veins M_2 and Rs, and by M_3 and M_4; but the reduction of redun-

dant cross veins, and the strengthening of the principal veins and brace seem to have been the means whereby these wings have attained thei goodly measure of efficiency.

Æschninæ.—We come now to a group that is flourishing in our ow time the world over. It contains the largest of our common dragon

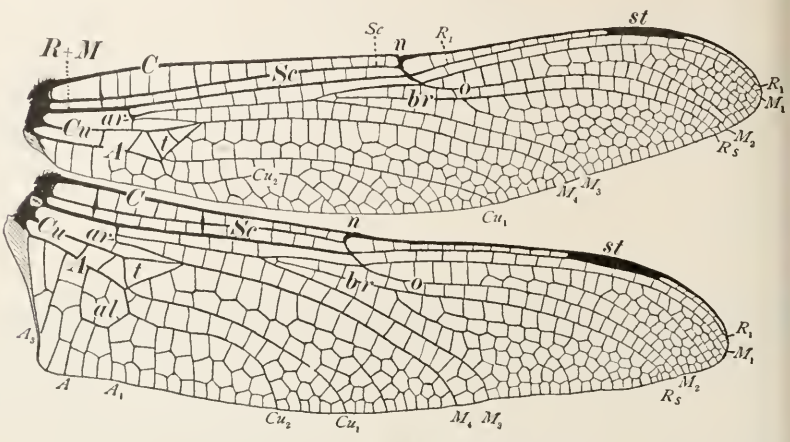


FIG. 25.—WINGS OF *Cordulegaster sayi* SELYS.

flies, all strong-flying species, composing many genera. In the more specialized genera are many species. There is great variety in the details of the luxuriant venation of the group. Here, then, we have opportunity to apply the facts of development previously outlined to the unravelling of a bit of genealogic history.

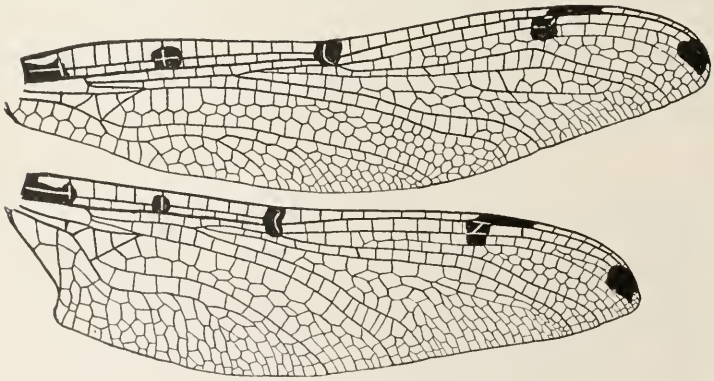


FIG. 26.—WINGS OF *Phyllopetalia apicalis* SELYS.

The most characteristic features of the Æschnine wing are (1) the approximation of veins M_1 and M_2, brought about by the bending forward of vein M_2 at the stigma, (2) the development of strong and broadly curved supplements, and (3) the elongation of the triangles in the direction of the axis of the wing. These will be seen in their best development in such genera as *Æschna* and *Anax* (Plate XL.)

Doubtless, the most generalized group within the Aeschnine series s composed of *Cymatophlebia* (fossil), and *Gomphæschna* (Plate XXXVII, fig. 1), which have the triangle little elongated, all supplements but little developed, the anal loop small and compact, with no supplemental loop, and the anal angle of the hind wing, therefore, not greatly dilated, but which always have the stigma braced against vein M_1 opposite a forward bend in vein M_2. These all exhibit affinities with the preceding and the next following groups. Even the upward bend of vein M_2 at the stigma is hardly more marked in *Gomphæschna* than in *Phyllopetalia* (fig. 26).

Passing by these two genera, we next come upon a number of others which have a more pronounced Æschnine aspect, as *Boyeria* (Plate XXXVII, fig. 3), *Basiæschna* (Plate XXXVII, fig. 2), and *Hoplonæschna* (Plate XXXVIII, fig. 1). These have vein M_2 more strongly bent toward the stigma, the triangles longer, radial and median supplements well developed, and trigonal supplement and supplementary anal loop developing. In these genera the radial sector is not forked.

In *Æschna* and its nearest allies (Plate XL) we see the further progress of these tendencies. There is this added feature—the radial sector has become forked. It will be observed that the anterior branch of this fork is separated from vein M_2 by a single row of cells, and that in the same place in *Basiæschna* (Plate XXXVII, fig. 2) there is a line of cross veins tending to straighten out. The anterior branch of the fork is developed out of this line of cross veins. In the Australian *Æschna brevistyla* (not figured herein) all stages of its completeness and incompleteness may be found in a series of specimens. In the nymphal wing of *Anax junius*, a strong trachea is seen to precede only the posterior branch of the fork. Thus the anterior branch of the fork is clearly a relatively recent acquisition of such genera as *Æschna*, *Gynacantha* and *Anax*, the dominant genera of the subfamily.

In tracing this relatively simple developmental line that leads to the highest specialization of this kind to be found, we have purposely passed by several lateral offshoots. The one of these which seems nearest allied to *Æschna* is represented by *Neuræschna* and *Staurophlebia* (Plate XXXIX, fig. 2), which, having retained the tip of the subcosta which extended beyond the nodus and many cross veins in important spaces, are not to be derived directly from forms in which these have been lost; lacking a brace to the stigma, can not have sprung directly from such genera as those of the Boyeria group in which this useful structure is well developed, but may well have sprung from the common ancestor of *Boyeria* and *Æschna*.

Furthermore, *Anax* (Plate XL, fig. 3), while very highly specialized, has retained the most primitive position of the media at the arculus to be found in the group, and has the hind angle of the hind wing rounded,

and not angulated, in the male. These characters, together wit others found in other organs, give cause for setting apart *Anax* (wit *Hemianax*, Plate XXXVI, fig. 3) as constituting a different develop mental line from the one in which *Æschna* is found.

Then there is the important Brachytron group of genera (*Brachy tron* (Plate XXXVIII, fig. 2), *Æschnophlebia* (Plate XXXVIII, fig 3), *Planæschna*, *Caliæschna*, *Nasiæschna* (Plate XXXIX, fig. 1 *Epiæschna*, etc.), which seems at first sight so closely allied to *Æschna* which was set apart by Karsch[a] for systematic purposes, on excellen venational characters, the manner and the purport of whose develop ment remain to be indicated. The radial sector is forked in these, bu after the anterior branch is acquired the whole sector does not, a in *Æschna*, bend anteriorly, arching away from the radial supplement which becomes bent in the opposite direction, but both remain straight and the tendency seems to be toward strengthening and deepening th fork. As a consequence, vein M_{1a} is allowed in the Brachytron grou to occupy its accustomed place and to bear its share in the stress o the wing stroke, not being crowded out, as in the Æschna group, b the encroaching distal end of vein M_2.

Boyeria seems to stand near where was the parting of the ways tha led to the development of these two groups. One may see that eithe form of radial sector might readily have been derived from that o *Boyeria* (Plate XXXVII, fig. 3).

The study of the trigonal supplement adds force to such opinion In *Boyeria* it might be interpreted as joining the median supplement or as passing below it with a single row of cells between; its positio is not decided. But in the Æschna group it distinctly joins th median supplement, and in the Brachytron group it distinctly extend below by one row of cells.

The behavior of the distal ends of veins M_3 and M_4 offers stil further corroborative testimony. Beginning with a condition lik that found in *Boyeria*, where there are several rows of cells include between these two veins for the distal third or fourth of their length the veins themselves being parallel, development takes place alon two distinct lines. In the Brachytron line these veins remain paralle and specialization consists in the progressive reduction of the cel between them to a single row. In the Æschna line, vein M_4 become bent away from vein M_3 at a point opposite the proximal end of th radial supplement, while reduction proceeds as usual on either side th place. (See *Æ. californica*, Plate XL, fig. 1, and *Æ. ingens*, Pla XL, fig. 2.) It will be observed that the vein M_4 finally appears to ru into vein M_3. This is wholly due to the increasing deflection of ve M_4 and to the straightening out of two cross veins which happen lie opposite the point of deflection. These cross veins first are

[a] Kritik des Systems der Æschniden, Ent. Nachr., XVII, pp. 273–290.

placed as to cause vein M_4 to appear forked (see *Æ. californica*, Plate XL, fig. 1), when they appear as the upper branch of that fork; finally they appear as the true continuation of the vein. As the anal vein is switched upon the second cubito-anal cross vein in the Libelulidæ, so here vein M_4 is switched into an entirely new position upon two cross veins.

It is worthy of passing remark that this shifting is an accompaniment of differentiation between longitudinal veins in very highly specialized Æschninæ. This will be much more clearly seen in actual wings than in the best of figures. A glance at such wings as those of *Anax junius* or *Æschna californica* will discover that Rs is strong, M_2 is weak; M_4 is strong, M_3 is weak; Cu_2 is strong, Cu_1 is weak. The strong vein bounds posteriorly the space in which the weaker one lies. The cross veins just discussed, which join vein M_4 so solidly to vein M_3, together with several lines of cross veins descending from the strongest part of the radial sector, complete the boundary of the space in which the weakest part of vein M_3 is included.

But to return to our theme, we have seen that the behavior of radial sector and supplement, of trigonal supplement, and the distal ends of veins M_3 and M_4 furnish cumulative testimony to two divergent lines of development, which, starting with forms a little less Æschna-like than *Boyeria*, have evolved the groups of *Brachytron* and *Æschna*. And we have shown that, with respect to venation at least, the groups of *Neuræschna*, *Anax*, and *Gomphæschna* are successively more remote.

Gomphinæ.—In this group we come upon another type of Æschnid venation, a type which is chiefly characterized by the similar shifting of the anal vein in both wings, but only to such extent that that vein appears more or less symmetrically forked. There are few venational specialties. Neither the shifting of veins for advantage of position nor the reduction of cross veins have proceeded very far. That venation is at a standstill is indicated by the unusual constancy of mechanically unimportant cross veins, such, for instance, as the one traversing the supertriangle. Variation from the type is slight, considering the large number of genera in the group; and such as there is, it does not lend itself readily to serial arrangement. The very moderately widened anal angle of the hind wing is supported mainly by straight and parallel anal and cubital branches, as in the more generalized Æschninæ. An anal loop is developed in many genera, but has so different aspect in several of them it seems quite possible it may have been developed several times independently. (See *Lanthus*, Plate XXXV, fig. 3; *Cyclophylla*, Plate XXXIV, fig. 1, and *Hagenius*, fig. 23.) A strong trigonal supplement is developed in *Hagenius*. The declined portion of the cubitus (inner side of the triangle) becomes elongated in the fore wing more than in the hind in *Cyclophylla* and *Aphylla* (Plate XXXIII, fig. 3). Accessory sectors of unusual strength

are developed upon the posterior side of veins *Rs* and M_4 in *Gomphidi* (Plate XXXIV, fig. 3). Possibly these features indicate the tips o numerous short developmental twigs. The brief records of the severa parts are certainly contradictory; and the parts themselves, which on might use as bases for the first divisions of the group, seem so nearl of equivalent importance that one may hardly choose between ther with assurance. Probably the records of other organs will be mor easy of interpretation.

The South American genus *Agriogomphus* (fig. 27) exhibits vena tional characters that are quite as generalized as are to be found in th group. Triangle and subtriangle are still four-sided, the cubital an anal veins before them being but moderately angulated, the stigma i weakly braced, there is no anal loop and there are no supplements.

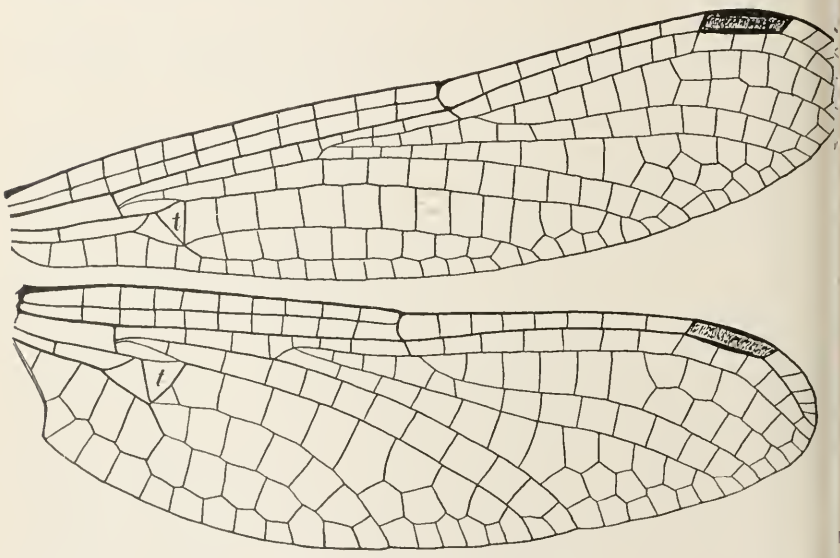


FIG. 27.—WINGS OF *Agriogomphus* SP?

We may remark, in passing, that the Gomphinæ, having attained fair measure of advantageous vein arrangement, and a fair (or, in th strongest species, even a superior) degree of vein differentiation, seer to have turned to a specialization of another sort. The imagoes are o the wing less constantly than other Odonata and fly for a shorter perio During this time their chief concern is with reproduction, hence w find the external genitalia highly specialized. The shortening of th period of imaginal life is correlated, also, with extreme specializatio of the nymph. In fact, the struggle for existence has been mainl transferred to nymphal life.[a]

[a] I have discussed this mattter more at length in my paper, Preliminary studies North American Gomphinæ, Can. Ent., XXIX, 164–168, 1897.

Petalurinæ.—The type of venation presented by this singular group parallels, rather remotely, the Libellulidæ in the behavior of the anal vein, shifting as it does upon the second cubito-anal cross vein to brace the antero-internal angle of the triangle in the fore wing, retaining a more direct course to the hind angle in the hind wing. It parallels the fossil *Stenophlebia* in the curvature of the wing outlines, tending toward a somewhat sickle-shaped wing apex. The very peculiar, narrowly linear stigma is directly correlated with the wing form. It will be observed in the genera *Uropetala* (fig. 4, *s*) and Phenes, in which the costal space is most narrowed and the stigma most curved and elongated, the brace vein has migrated away from the stigma toward the nodus. In this group the anal loop is often not well differentiated (fig. 28). Excepting at the base of the wing, reduction of cross-veins has not been carried very far. *Tachopteryx hugeni* (fig. 29) seems to be the most generalized living member of the group (compare with Plate XXXVI, fig. 1). It will be observed this one is most like the Gomphinæ, the subfamily which is doubtless nearest akin. The group is a very small one, apparently on the wane.

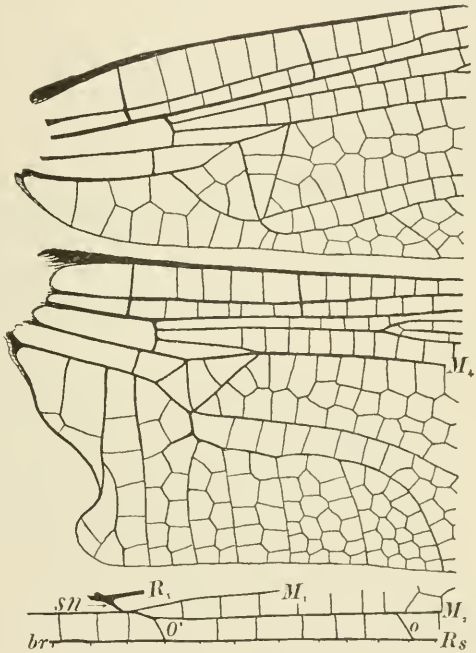


FIG. 28.—BASES OF WINGS OF *Petalura gigantea* LEACH, AND A DETAIL FROM THE REGION OF THE NODUS, SHOWING THE BRIDGE WITH TWO OBLIQUE VEINS, O' AND O.

It is well represented among the Tertiary fossils of Europe. Of living species there is one in the eastern United States, one in Nevada, one in Japan, and there are several each in Chile and the Australian region.

B. Libellulidæ.—This family, unlike the Æschnidæ, exhibits a single type of venation, whose dominant tendency is toward the differentiation between the wings, by means of the procession of the triangle, and the switching of the anal vein in the fore wing, and in the hind wing the recession of the triangle and the elongation of the anal loop. The stigma is never braced, and the bridge remains shorter than in the Æschnidæ, with fewer included cross veins.

Macromiinæ.—Members of this group (Plate XLI, figs. 1 and 2) have followed these tendencies a little way, and have then gone off on

lines of their own, specializing highly. The shifting of the anal vein in the fore wing, the fusion of the branches of the media beyond the areulus, the development of a strong anal loop (of almost Cordulegasterine form, to be sure), the retraction of the nodus in the hind wing, and especially the general reduction of cross veins and the narrowing of the apex of the wing, mark this as a peculiar group, more distinct than any other within the Libellulid series, and well worthy of subfamily rank.

Libellulinæ, including Cordulinæ, s. str.—Passing *Macromia*, and passing also a few isolated forms with triangles in the fore wing four sided and in the hind wing often little retracted and with the anal loop short, indistinct, or wanting[a]—all lateral offshoots, I believe, from near the bottom of the Libellulid series—we come upon a series of closely related forms, the most extensive and flourishing in the order. It were idle to attempt to indicate all the lines of specialization to be

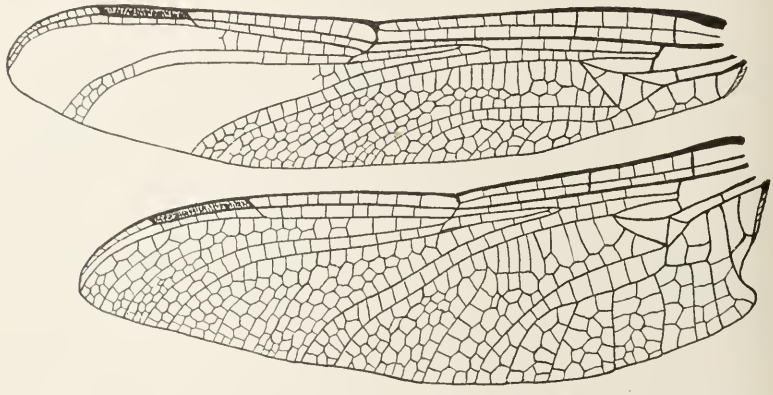


FIG. 29.—WINGS OF *Tachopteryx hageni* SELYS, DETAILS IN PART OMITTED IN FORE WING.

found in the wings of this series. We will endeavor to point out only a few of the leading tendencies that are superadded to the more general ones already noticed.

It is most interesting to note, in this series, how the two venation-evolving processes already discussed, vein adjustment and vein differentiation, have alternately held sway. Thus, in the first instance, vein adjustment has been carried out to a very moderate extent, vein differ-

[a] I pass these by because I have not found the genetic thread that will bind them into a natural series. I have seen but few of them (*Tetrathemis*, fig. 10; *Nannodythemis*, *Nannothemis* (Plate XLIII, fig. 2), *Nannodiplax*, and *Nannophya*), and in this paper we are dealing only with lines of development. These are among the rarest of specimens in collections, and differ so much among themselves that there are of them almost as many genera as species. They have all the earmarks of developmental remnants. If Karsch's group *Nannophyæ* (Ent. Nachr., XV, pp. 245–263) should be made to include all these forms, it should include also *Cordulephya* and perhaps *Idyonyx*, which have more affinity with some of these than with any of the Cordulinæ proper.

entiation to a remarkable extent, and the result has been the evolution of the Corduliinæ, *s. str.* (Plate XLII.) The branches of the media are never extensively fused at their departure from the arculus. The true course of the anal vein behind the triangle is never obscured. The anal loop never becomes distinctly foot shaped. It is short in *Gomphomacromia* (Plate XLIII, fig. 1); longer and shaped like the conventional diagram of a simple gland in *Oxygastra* (Plate XLII, fig. 2), truncated on the end but not widened in *Neocordulia androgynis* (Plate XLII, fig. 1); squarely truncated and slightly widened in the undescribed *Neocordulia* shown in fig. 30; and obliquely truncate and increasingly widened on the "toe" side in *Hemicordulia* (Plate XLII, fig. 3), *Somatochlora*, etc. In short, the vein shifting of the Libellulidæ is far from reaching its maximum in this group, but a fairly

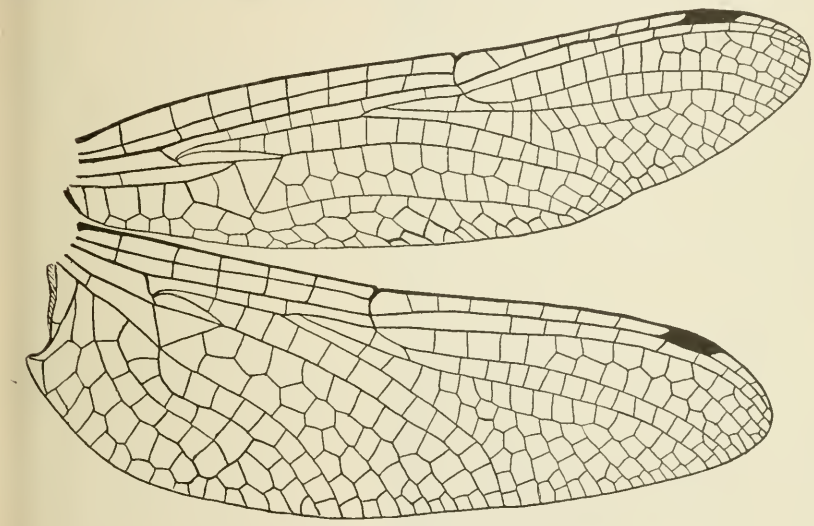


FIG. 30.—WINGS OF AN UNDESCRIBED SPECIES OF *Neocordulia* FROM BRAZIL.

advantageous arrangement of the veins has been attained, and reduction of unimportant and strengthening of important veins has proceeded until the Corduline wing has become the equal in efficiency of the best of insect wings and the superior of most others in its own family.

Among Libellulinæ proper, *Agrionoptera* and its nearest allies seem, on the whole, about as generalized as any (Plate XLIV, figs. 1–3) in having cubitus and anal vein very moderately angulated before the triangle in the fore wing, slight recession of the triangle and a short anal loop in the hind wing, and in the form of the wing as a whole.

Passing up the series we find the triangles progressing along lines we have already pointed out, the anal loop becoming foot shaped, and extending a support for the ever-widening anal area. When it was just becoming foot shaped, with a rudimentary "toe" meeting the hind

margin of the wing, the hind angle only moderately enlarged, specialization by reduction seems again to have dominated, producing a group of genera of which *Macrothemis* is a good exponent (Plate XLVI, fig. 1).

Then there is the important group of genera allied to *Libellula*, in which the branches of the media at their departure from the arculus are hardly fused, in which the narrowing and transverse elongation of the triangle and the deflection of the anal vein before the triangle have progressed very far, but in which only a very moderate reduction of cross veins has occurred (Plate XLVIII). The tendency of vein M_2 to become undulate is also a feature of this group.

There is also the heterogeneous group of genera allied to *Neurothemis*. These will at least agree in exhibiting the highest degree of vein adjustment together with the lowest degree of vein reduction to be found in the series (fig. 18).

At some point in this series not remote from *Celithemis* (Plate XLVI, fig. 2) may have set in the extensive reduction of cross veins characteristic of a very large number of genera allied to *Sympetrum*. (See Plate XLVI, fig. 3, and Plate XLVII, fig. 1.)

Another offshoot from near the same place, combining in a high degree both kinds of specialization, culminates in *Tramea* and its allies (Plate XLIX), which I regard the most specialized of Libellulinæ, if not of all Odonata.

In the three last-mentioned groups there is a pretty adjustment of the second cross vein in the space between veins M_1 and M_2 in opposition to the proximal end of the radial supplement. Plates XLV and XLVI and fig. 2 of Plate XLVII will show its increasing definiteness and obliquity of position and the perfecting of the brace of which it is a third part, the other parts being the supplement and the oblique vein. A trivial character this? Indeed it is but a straw, yet it shows the way biologic winds blow.

ZYGOPTERA.

In this suborder we have again two families, the more generalized abounding, as before, in venational experiments (if I may so speak), some of which have been abandoned in recent times, the more specialized, being more homogeneous, characterized by a single principal trend in its wing development. The suborder as a whole has retained in recent times two primitive characters, in the similarity of fore and hind wings[a] and in the total lack of supplements.

1. *Calopterygidæ*.—There are four fairly distinct types of venation in this family, the most peculiar of which is represented by the fossil genus *Isophlebia* (fig. 31). In this type the hind wing was as much dilated at the base as in the Anisoptera, but by very different means.

[a] For this reason we figure in most cases but one wing.

The support for the expanded area developed upon vein Cu_2, which was set off from vein Cu_1 by a long posteriorly directed stalk; secondary branches developed upon the posterior side of vein Cu_2 radiating to the wing margin. The anal vein did not join vein Cu_2. The stigma was unbraced, and the wings were decurved at the tips, much as in the Petalurinæ.

Among living Calopterygidæ the tendency has been to match cross veins in lines parallel with the veins, thus producing a large number of interpolated sectors between the principal veins. This has been carried so far that few vestiges of the primitively hexagonal form of the cells remain. This has facilitated (perhaps we should say has accompanied) the throwing of the wing membrane into longitudinal furrows, and we find the sectors, in some forms, alternately convex and concave even to the distal margin of the wing. In those forms in which the furrowing of the membrane is most general we find the least tendency toward reduction of cross veins. Perhaps the fanlike folding of the membrane enabled it to resist bending and rendered unnecessary the differentiation of stronger veins for that purpose.

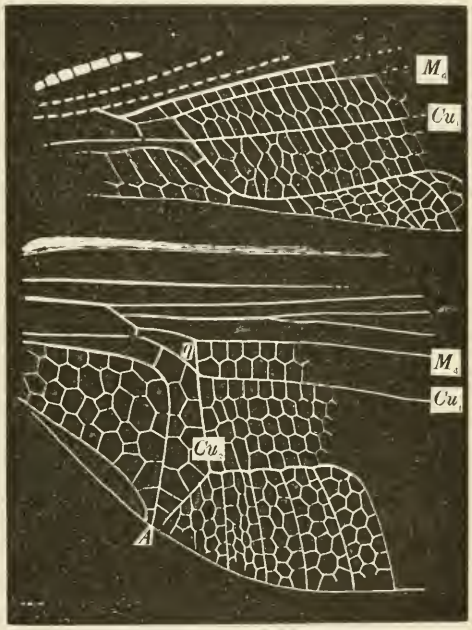


FIG. 31.—BASE OF WINGS OF *Isophlepia* (FOSSIL) IN PART AFTER DEICHMÜLLER.

Epallaginæ.—This group comprises the more generalized living members of the family, especially in the Legion Euphæa of de Selys, wherein the nymphs, so far as known, have paired gill filaments along the sides of the abdomen and have biramous mandibles. In this group the media tends to descend to the middle of the arculus, the nodus to recede moderately toward the base of the wing, and the quadrangle to lose the dividing cross vein. The quadrangle behaves similarly in both fore and hind wings. *Pseudophæa* seems, on the whole, as primitive as any genus of the group (fig. 32). *Rhinocypha* and its allies (Plate LII, figs. 1, 2, and 5) constitute a short lateral series. De Selys long ago showed, from characters not drawn from the wings, that they constitute a distinct subordinate group, but he did not point out the venational characters in which they are peculiar. These will be dis-

covered by observing the behavior of the medial and cubital branches just after their separation. Just beyond the arculus veins M_{1+2} and M_3 separate by arching in opposite directions, forming a symmetrical fork. At the end of the quadrangle vein M_4 arches forward, vein Cu_1 sometimes arching with it, and vein Cu_2 arches backward, the two thus becoming set in opposing positions. Vein Cu_2 remains simple.

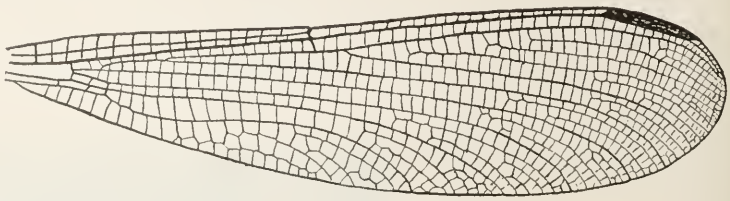


FIG. 32.—WING OF *Pseudophæa sp?*

Throughout the group the stigma is well developed. In the space between veins M_1 and M_2 the longest of the sectors occupies an intermediate position, with shorter sectors on either side of it. The South American *Cyanocharis* (Plate LI, fig. 3) and *Dicterias* parallel the next following group in the fusion of vein M_{1-3} with the radius beyond the arculus, but in general the group is wholly lacking in those peculiar developments that characterize the two next groups.

Anisopleura, *Epallage* (Plate LI, fig. 2), *Bayadera*, *Cyanocharis* (Plate

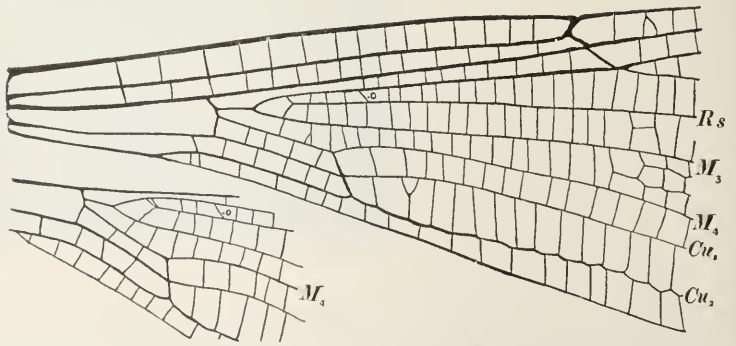


FIG. 33.—BASE OF FOREWING AND A BIT OF HINDWING OF *Rhinocypha sp?* *o*, OBLIQUE VEIN THAT WORKS THE POINT OF SEPARATION OF THE TRACHEA OF THE RADIAL SECTOR.

LI, fig. 3), *Diphlebia*, and *Philoganga* (fig. 44) illustrate a tendency toward the reduction of the base of the wing, and toward a considerable degree of vein differentiation throughout the membrane. The general result is analogous to that arrived at in the Agrioninæ, discussed below.

Vestalinæ.—In all this extensive group the media descends the arculus and departs from it in a line that is continued directly by vein M_3, while vein M_{1+2} arches strongly from its anterior side. The

fork is thus unilateral. In such genera as *Calopteryx* (fig. 34) and *Vestalis* (fig. 41), vein M_{1+2} reunites with the radius—completely fuses with it—only to separate again, after which its base appears as a cross vein and its distal end as a branch of the radius.[a] The longest of the sectors between veins M_1 and M_2 closely parallels vein M_2, with all the shorter sectors before it. The stigma tends to atrophy, more rapidly in the males. The quadrangle becomes unusually elongated, and is almost always convex on its anterior side and traversed by a number of cross veins, among which the identity of the typical one is never evident. Vein Cu_2, just beyond the quadrangle, sets off a recur-

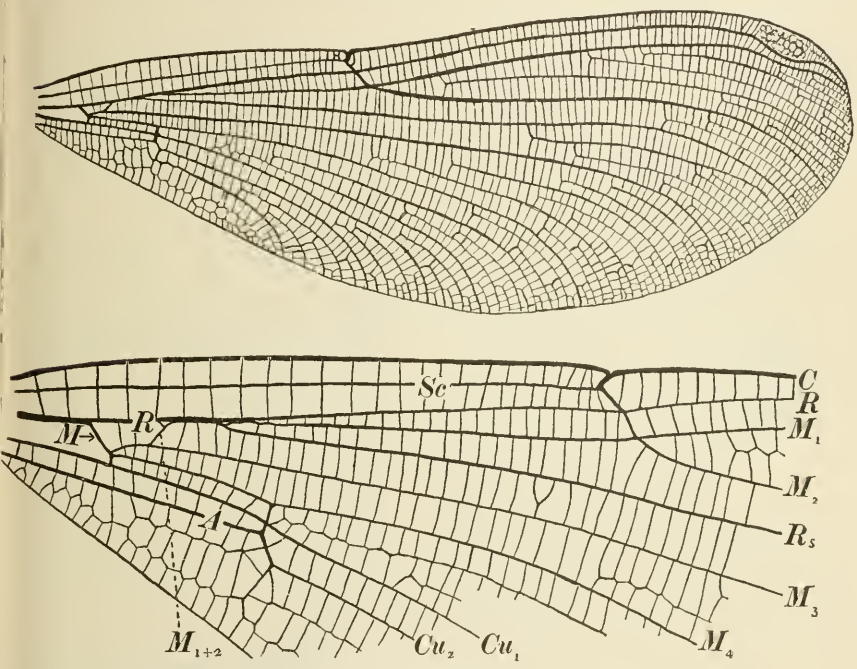


FIG. 34.—*Calopteryx maculata* BEAUVOIS, FORE WING AND BASE OF HIND WING.

rent branch for the support of the anal angle of the wing. The longer interpolated sectors tend to become attached as forks to the front side of the principal veins, and to become set in opposition to the same beyond the point of their attachment. *Vestalis* (fig. 41) illustrates well the culmination of nearly all of these tendencies.

A short side line includes only *Hetærina* and *Lais*. The tendency in these is neither toward narrowing the wing at the base nor widening it beyond; but it is found evolving a unique transverse wing brace out of the bases of the cubital branches. (Plate LI, fig. 4.)

[a] Thus the radius gained its typical complement of branches, which enabled Redtenbacher to see in *Calopteryx* the form of wing from which all other Odonate wings might be derived! (Ann. k. k. naturhist. Hofmus. Wien, I, 1886, p. 167.)

The main line includes such forms as *Phaon*, *Mnais*, *Calopteryx* (fig. 34), *Neurobasis* (fig. 43), and *Vestalis* (fig. 41), in which the tendency is toward further vein adjustment without much further vein differentiation; attaching sectors to principal veins, and widening the wing distally, losing the stigma.

Thorinæ.—Another type of venation is found in *Thore* (fig. 35) and its allies, a very circumscribed group, comprising but a few South American genera. De Selys long ago set this group apart upon an excellent venational character, i. e., the media does not descend the arculus at all. To this may be added, the media departs from the arculus in line with its branch M_1, while M_3 arches strongly from its posterior side, thus making a unilateral fork which is in position the reverse of that of the Vestalinæ. The longest of the sectors between veins M_1 and M_2 closely parallels vein M_1, with all the shorter sectors behind it. The basal curvature of vein M_4 makes the quadrangle concave anteriorly, and widest at the proximal end. There is an odd differentiation between quadrangles of fore and hind wings, that of the latter becoming twice the length of that of the former. In *Cora* (fig. 36) vein Cu_2 is almost simple; in *Thore*, *Euthore*, and *Chalcopteryx* it is symmetrically forked just beyond the quadrangle.

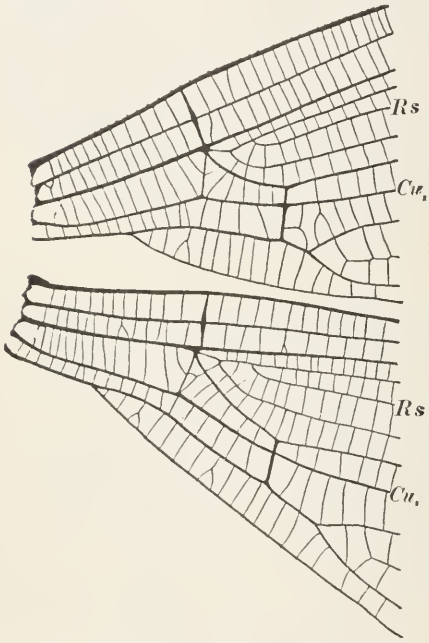


FIG. 35.—BASE OF WINGS OF *Thore gigantea* SEL.

While in this group a form and general aspect of wing much like that of the typical Calopteryginæ has been developed, a comparison of the venational characters will show that the means employed have been almost diametrically opposite.

Some synthetic types.—In Plate XLI, fig. 3, there is shown a new figure of the much-discussed *Palæophlebia superstes* Selys, from Japan—fore and hind wing of a female specimen, photo-enlarged. It is by no means easy to indicate the nearest relationship of this isolated species. Wing characters, like other characters, are contradictory. It agrees with the Lestinæ and with the more generalized members of de Selys's heterogeneous and untenable Legion Podagrion in the form of the stigma and arrangement of cross veins behind it, and in the arrangement of the interpolated sectors in the space between veins M_1 and M_2, and also in the obliquely placed quadrangles. It agrees further with Lestinæ in the possession of a long bridge terminated

distally by an oblique vein. It differs utterly, however, in the form of the quadrangle of the hind wing, in the remoteness of the nodus from the arculus, and in the relation of the arculus to the hypertrophied antenodal cross veins.

It agrees with generalized Gomphines in the last-named particular (compare with Plate XXXV, fig. 3), also in the general relations of bridge and oblique vein, and relations between arculus and nodus; but its quadrangles are undivided, and the hind margin of both wings is utterly unlike all known Anisoptera. In having a quadrangle that is obliquely placed, narrowing distally in the fore wing and widening distally in the hind wing and undivided in both, it stands entirely alone.

De Selys pointed out when he described the species that it showed striking resemblance to the fossil genus *Heterophlebia*—a genus, unfortunately, still insufficiently known. The quadrangle of the fore wing is, in fact, practically identical; and other parts of the wing, so far as known (whether there were hypertrophied antenodals is uncertain), are similar. But the quadrangle of the hind wing in *Heterophlebia* is very different. The cubitus, instead of being declined before the

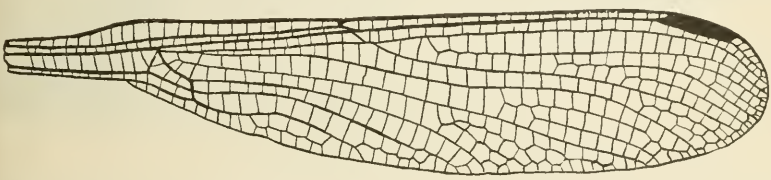


FIG. 36.—HIND WING OF *Cora incana* HAGEN.

quadrangle as in *Palæophlebia*, is bent at the middle of its posterior side, and from that point springs the dividing cross vein, as in Anisoptera; and the cross vein is declined so far that it rests against the upper end of the terminal cross vein of the quadrangle. There is yet another point of difference, of perhaps even greater importance. The bridge at its inner end is directed toward and attached to vein M_3 in *Heterophlebia*, whereas it turns the other way and attaches to vein M_{1+2} in *Palæophlebia* and in all living Odonata. (Although in the more generalized Gomphinæ it is apparently symmetrically forked and not turned either way, whenever the fork happens to be unsymmetrical the leaning is seen to be toward the anterior side.) This is a difference of kind that is not to be passed over lightly.

Heterophlebia shares this peculiarity with one other genus, *Tarsophlebia*, likewise fossil, and it is a strong bond of union between them, of more importance than their rather striking differences, these being mainly differences of degree. *Tarsophlebia*[a] has the quadrangles

[a] *Libellula pannewitziana* Göppert belongs in *Tarsophlebia*, as will be seen by comparing Assman's figure of the type (Zeitschr. für Entomologie, I (n. s.), 1870, pl. I, fig. 11) with fig. 3 of Hagen's plate cited herewith. *Heterophlebia jucunda* Hagen is not a *Heterophlebia* at all, nor even nearly related thereto.

even more obliquely placed, similar in fore and hind wing, without the dividing cross vein, and also without the basal cross vein, so that the quadrangle is confluent with the basal space, much as in the fore wing of fig. 38. The space between veins M_1 and M_2 is narrower also, with a different arrangement of interpolated sectors. These characters are well shown[a] by Dr. Hagen, to whom we owe our best knowledge of these remarkable forms.

B. Agrionidæ.—This family is in essential agreement in all those venational characters which are most fundamental. The tendency throughout is toward extreme reduction of the anal area, making the wing "petiolate," and toward the matching of cross veins in transverse lines. The antenodal cross veins are almost always reduced to two. The nodus is greatly retracted and the quadrangle approximated to it. The media does not descend the arculus.

Lestinæ.—This group is quite unique in its own family in one character that has been already indicated, the radial sector fuses with vein M_2 for a long space, and an oblique vein and a very long bridge, reaching more than halfway from the nodus to the arculus, are preserved. Nodus and quadrangle are but moderately approximated, and the matching of cross veins seems only begun (see Plates LI, figs. 6 and 7, and LIII, fig. 1).

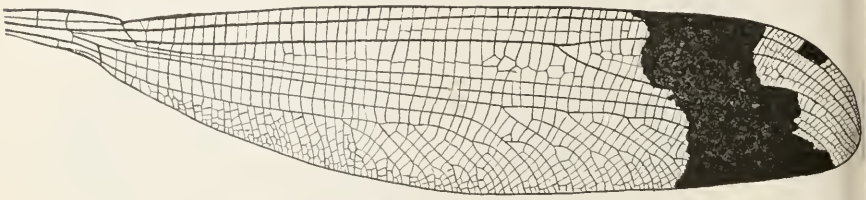


FIG. 37.—WING OF *Megaloprepus cerulcatus* DRURY.

Anormostigmatini.—In this curious group the radial sector leaves vein M_2 at the subnodus, and nodus and quadrangle are quite approximate. The part of the wing beyond the nodus becomes very greatly enlarged. The stigma is never braced; on the other hand, it becomes diffuse or is lost. Cross veins fall into transverse lines over a considerable part of the wing (Plate LI, fig. 8), especially in the smaller species, and interpolated longitudinal sectors in *Megaloprepus* (fig. 37) and *Microstigma* become attached to principal veins, of which they then appear as branches. In the space between veins M_1 and M_2 the longest sector parallels vein M_2. Here the retraction of the nodus toward the base of the wing and the migration of the base of vein M_2 outward toward the stigma have attained their maximum. These are among the most grotesquely specialized of living insects.[b]

[a] Palæontographica, XV, 1866, pl. II.

[b] Since this paper was written the venation of the genus *Thaumatoneuria* has become known to me through Dr. Calvert's figures (Biol. Centr. Amer., Neur., pl.

Agrioninæ.—This group contains a larger number of genera and species than any other of equal homogeneity of venational characters. The radial sector leaves vein M_2 near the nodus (sometimes following vein M_2 in its migration along vein M_1 toward the stigma), and nodus and quadrangle tend to close approximation. Cross veins are generally matched in transverse lines, and the stigma is generally strongly braced.

Two minor lines of development may be briefly indicated in passing: One, tending toward the loss of the branches of the cubitus—*Pulæmna* (Plate LIII, fig. 2), *Platysticta* (Plate LIII, fig. 3), *Disparoneura* (Plate LIV, fig. 2), *Idioneura* (Plate LIV, fig. 3), and *Cænoneura* (Plate LIV, fig. 4); and a second, including nearly the whole of the group which lacked this tendency, but in which nodus and quadrangle become more and more approximate, and the veins M_2, R_s, and M_3 migrate separately along vein M_1 from their accustomed places toward the stigma (Plate LIII, figs. 4, 5, and 6), or in which progress has consisted in

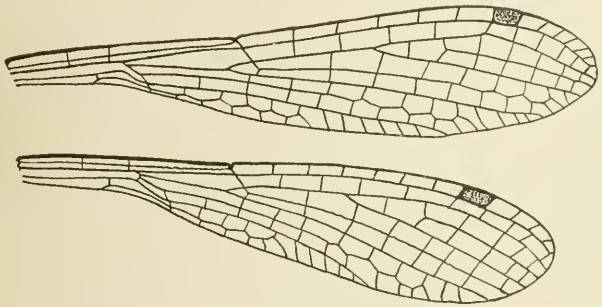


Fig. 38.—Wings of *Hemiphlebia mirabilis* Selys.

mere reduction of cross veins and better matching of them in transverse lines, and in the perfecting braces at the nodus and elsewhere.

This series furnishes in the genus *Hemiphlebia* (fig. 38) a striking example of the loss of a cross vein that is elsewhere very constant—the

III, figs. 16 and 21). I think *Thaumatoneuria* belongs here; it has all the essential venational characters of this group, and surely these are sufficiently distinctive. It is more generalized than *Megaloprepus*, in that vein M_2 has made less progress along vein M_1 away from the nodus, some vestiges of the primeval extra antenodal cross veins are preserved, most of the interpolated sectors are still unattached to the veins, and the stigma is larger and better preserved. It is a curious and probably significant fact that in the two series of Zygoptera—Vestalinæ and Anormostigmatinæ—in which the long sector between veins M_1 and M_2 parallels M_2 should be the only ones in which the stigma progressively dwindles and disappears. It is conceivable that the stigma might lose importance for want of the support that this sector would give if approximated to it at the apical bend. Perhaps the concavity on the costa in *Mecistogaster lucretia* (Plate LI, fig. 8) and the conjoining and the sharp bending backward of the veins behind it may be a unique way of supplying such deficiency of bracing, preserving the utility of the stigma as a weighted striking point toward the end of the cutting edge of the wing.

cross vein forming the lower end of the arculus.[a] This is entirel absent from the fore wing of the males; it is present, however, in th hind wing of both sexes, and often also in the fore wing of the femal The loss of this cross vein has resulted from a shift of other veins an a consequent shift of responsibility in stress of wing stroke. Th symmetrical fork formed at the separation of veins M_{1+2} and M_3 (else where always unilateral unless the fork be very narrow) and the upwar bend of the anal vein at its departure from the hind margin, to mee the cubito-anal cross vein and the very considerable progression of th arculus beyond the second antenodal, are the visible signs of the reac justment which has relieved the basal side of the quadrangle of i former responsibility.

It is needless to remark after observing the form of the wings, tha among the Zygoptera there are no strong flying species. Most o them fly so low over the surface of the water that their winge enemies can not safely descend to their level. The Lestinæ live ami sheltering semiaquatic vegetation. Vestalinæ seem not to be desire for food; their coloring may suggest that they are not good eating The action of the wings is that of sculling solely; only the distal po tion of the wing which takes the active part in insects' flight is we developed. There is no soaring basal aeroplane, as in the Anisopter to support the body passively by merely gliding upon the resistant ai

I offer below a scheme of subfamilies for the order, which seems t me to be, in the light of the evidence that present knowledge of ven tion affords, an approximation toward equivalent values for the groups. The weakest distinction seems to me to be between the Co dulinæ and the Libellulinæ; the most doubtful association of recen forms that of *Cordulegaster* and *Petalia* together. The fossil grou seem not only more isolated but also more strongly characterize structurally than the others.

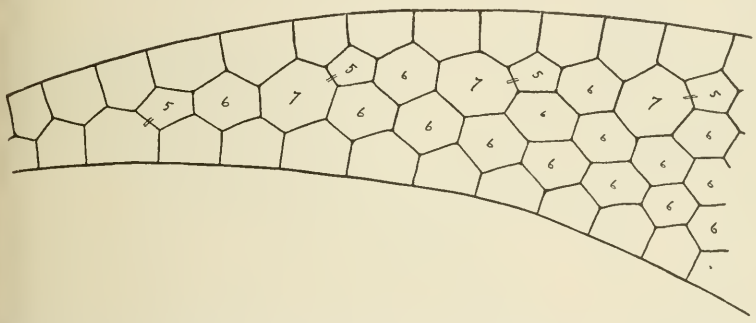
- *Anisoptera.*
  - Æschnidæ.
    1. *Gomphinæ* (recent and fossil).
    2. *Petalurinæ* (recent and fossil).
    3. *Stenophlebiinæ* (fossil).
    4. *Cordulegasterinæ* (recent and fossil).
    5. *Chlorogomphinæ* (recent).
    6. *Æschninæ* (recent and fossil).
    7. *Æschnidiinæ* (fossil).
  - Libellulidæ.
    8. *Macromiinæ* (recent).
    9. *Cordulinæ* (recent and fossil).
    10. *Libellulinæ* (recent and fossil).
- *Zygoptera.*
  - Calopterygidæ.
    11. *Heterophlebinæ* (fossil).
    12. *Palæophlebinæ* (recent).
    13. *Epallaginæ* (recent and fossil).
    14. *Vestalinæ* (recent).
    15. *Thorinæ* (recent).
  - Agrionidæ.
    16. *Lestinæ* (recent and fossil).
    17. *Agrioninæ* (recent and fossil).

[a] This arculus cross vein is absent in the fossil genus Tarsophlebia as already note

V. DYNAMIC CONTROL IN VEIN EVOLUTION.

So numerous are the evidences that veins are largely controlled in heir development by purely mechanical causes, it would be impossible, vere it not also undesirable, to enumerate them here. We have come pon parallelisms at every turn. We have seen essentially the same echanical feature of efficient wings made out of homologically dif- erent things repeatedly. But the adult wing is only a machine, and his was to have been expected. It remains now for us to notice a few eatures which indicate the operation in these wings of far-reaching echanical principles.

It is not at all surprising that we should find the first regular form aken on by the areoles of the wing to be hexagonal. The hexagon is ature's favorite plane figure, and there is a good mathematical reason vhy it should be so: economy is a good biological reason. We have



IG. 39.—DIAGRAM ILLUSTRATING A TYPICAL (HYPOTHETICAL) ARRANGEMENT OF THE AEROLES IN ONE OF THE WIDER SPACES OF THE WING.

lready shown that bordering, straight veins eliminate certain angles f the hexagons, converting them into pentagons and rectangles. We ass now to notice the arrangement of the areoles in the wider areas f the wing, where least influenced by the veins. The spaces between rincipal veins or branches of veins, widening distally, are filled prox- mally by a single row of rectangles or by a double row of alternating entagons. Actual hexagons are present only when there are three or nore rows of areoles included. The first cell in each added row is ypically a pentagon, which presents an angle to the cleft between the eparating rows of areoles and a straight side to meet succeeding hexa- gons. A triangle or a heptagon would of course do the same, but ot with so little disturbance of surrounding hexagons. Opposite the nitial pentagon an areole in one of the preexisting rows acquires an dditional side, becoming a heptagon (or a hexagon, of course, if it vere first a pentagon). Thus pentagon and heptagon are complemental, nd together initiate new rows of cells with the least possible disturb-

ance of the series of hexagons. The accompanying diagram (fig. 39 shows the ideal cell arrangement.[a]

I hasten now to add that a perfectly typical arrangement of th areoles throughout a single entire space in a dragon-fly wing I hav not found, although it is easy to find in many of the more generalize forms ample evidence of the operatio of the principle. The accompanyin drawing (fig. 40) of parts of actua wings will serve for illustration. have made no hunt for better, for thes show, also, why the typical conditio is so early lost. Accessory trachea branches penetrate along broken line of cross veins, bringing them into line then supplements are superadded, an the havoc of the hexagons is complete Enough of the typical arrangement fo recognition is to be looked for only i wings lacking strong accessory trachea branches and supplements.

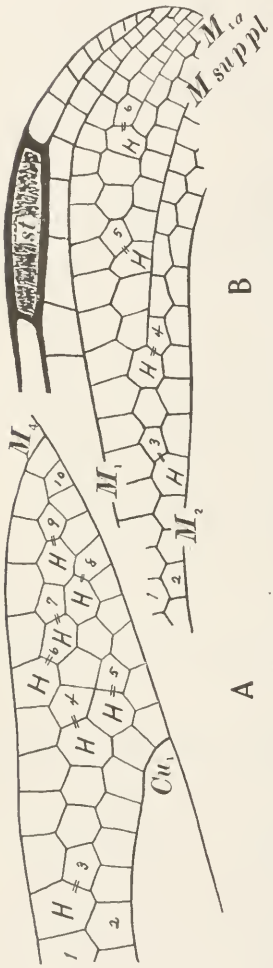


FIG. 40.—DRAWING OF PARTS OF WINGS, SHOWING THE ACTUAL CELL ARRANGEMENT. *A. Epigomphus paludosus*; *B. Agrionoptera insignis*. INITIAL CELLS ARE NUMBERED IN THE ORDER OF THE INTRODUCTION OF THEIR SEVERAL ROWS; HEPTAGONS ARE MARKED WITH AN H.

Tissue cells often appear hexagona in section, and when crowded into sim ilarly shaped areas, often behave a do these areoles of dragon-flies' wings The histologist who looks over the plate accompanying this paper will not fa to see here and there groups of areol showing conformation entirely compar able to familiar images of tissue cells

Coming now to some points whic have to do probably only with wing and with aerial navigation, we reca that a form of wing broad at base an narrow and pointed at the apex, we known for its efficiency in insects ger erally, we have seen developed twic upon two very different plans, culm nating in *Anax* and *Tramea* respectively. Both have adjusted th wing apex to a degree of rigidity on the costal margin, and of plianc behind it, which gives the greatest resultant in forward motion fo

[a] Dr. R. T. Jackson has shown (Bull. Geol. Soc. Amer., VIII, 1896, p. 164) that th interambulacral plates of sea urchins are potential hexagons, that the border ro are pentagons—hexagons, with one angle eliminated, as here—and that pentagon a heptagon together initiate new rows of plates. Practically the only difference betwe the typical arrangement of these areoles and that of the interambulacral plates, figured by Dr. Jackson, arises out of the difference in the shape of the areas to be occ

rapid vibration in air. Both have developed at the wing base close against the body a broad soaring surface, an aero-plane, which in rapid flight supports the weight of the body upon the resistant air. Wings of broad base and pointed apex are characteristic of other insects of rapid flight, but in most others (hawk moths, cicadas, bees, etc.) the two wings are united and used as one. The basal expanse is secured by shortening the hind wing and directing it posteriorly. Different as are the wings of birds, these also are sharply pointed in the species of swiftest flight (ducks, swallows, etc.). I can not state the aeronautic principle involved in the pointed wing, but I ask no better proof of its existence than is furnished by the efficiency of such a wing and its repeated independent development.

In the arrangement of the principal veins we have called attention to the fact that the Odonata, except in the earliest stages, differ very widely from all other insects. There is hardly a group from which they differ more in fundamental plan than the Ascalaphidæ. The latter

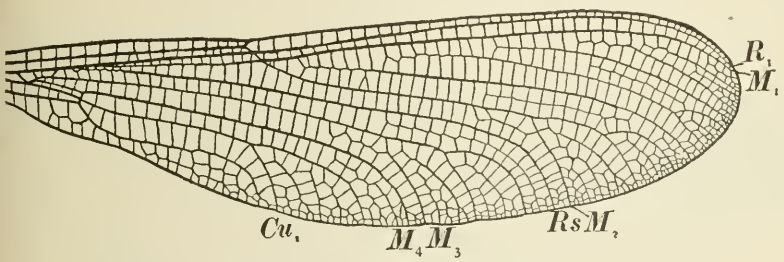


FIG. 41.—WING OF *Vestalis amoena* SELYS.

have the radial sector enormously developed and in its accustomed place, occupying the central field of the wing, while the media is greatly reduced; in the Odonata the development of these parts is reversed and the radial sector is out of place. The differences at the costal border of the wings is so great that I will only invite comparison of the Ascalaphid wing in Plate XXXVI, fig. 2, with the wing of any dragon-fly. If now, without reference to homologies, we examine this wing of *Ulula*, we will see in it familiar mechanical features. (1) From the stigma there extends obliquely across the wing tip to the posterior margin a vein which occupies the position, and probably performs the function, of the vein M_{1a} in the Odonata. (2) Intersecting the wing obliquely, so as to mark off a basal posterior third

pied in the two cases. In the echinoderm the area is symmetrical, and new rows are introduced alternately on the two sides. In the dragon-fly wing the space is unilateral, as shown in the diagram, and the rows are introduced chiefly upon the anterior, convex side. The principle is the same; but we should not omit to notice how different are the two things whose arrangement it controls—in the one case, solid plates; in the other, a mere rim of solid matter surrounding an almost empty space.

of it, are two parallel veins, separated by a single row of cells, analogous to the veins M_3 and M_4 in the Odonata. (3) Behind these is a transverse bracing of the basal part of the wing, analogous to the triangle in the Anisoptera, and to the special braces beyond the quadrangle in *Lais* and *Hetærina*.

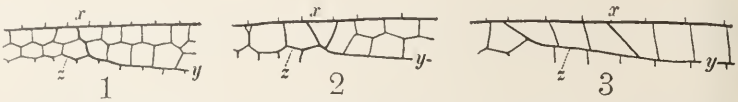


FIG. 42.—DIAGRAM (HYPOTHETICAL) OF THE EVOLYTION OF A BRACE FOR A UNILATERAL FORK; 1, 2, 3, SUCCESSIVE STAGES.

We have shown that the brace vein to the stigma and the supplements, etc., are independently developed in several groups. We have shown that the sectors interpolated between the tips of veins in several groups have become attached to veins, making the latter appear forked. Our illustrations of this were veins *Rs* in the Aeschninæ, and veins M_2 and M_4 in *Chalcopteryx* (fig. 22); but if one wishes to see how far

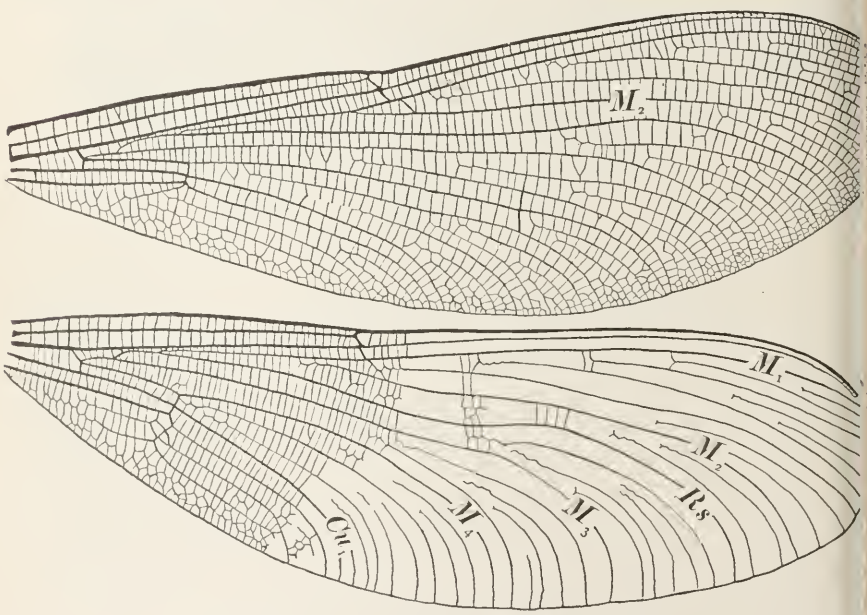


FIG. 43.—WINGS OF *Neurobasis kaupii* BRAUER.

this process has been carried on independent lines, let him examine such wings as those of *Megaloprepus* (fig. 37) and *Vestalis* (fig. 41).

There is one frequent tendency toward purely mechanical improvement of which we have given but a single example—the bridge, joining the radial sector to vein M_{1+2}. It is manifest always in a brace of the same kind as the one which we have technically designated as the bridge, and is formed at a point where a branch springs from the side of a straight vein and then bends parallel. The accompanying diagram

(fig. 42) shows how such a brace is evolved out of the boundaries of ordinary cells.

This brace joins the main vein with the elbow in the branch, thus correcting the mechanical weakness of the unilateral fork. Aside from the bridge, such a brace is developed in *Rhinocypha* (fig. 33), extending the attachment of vein *Rs* along vein M_{1+2} toward the arculus;[a] also, in *Chalcopteryx* and many Calopteryginæ; again, at the proximal end of vein M_2 in *Neurobasis* (fig. 43) and a few closely related genera,[b] as it was, also, in some fossil species referred to *Stenophlebia;* again, at the proximal end of vein M_{1a} in *Nasiæschna pentacantha* (Plate XXXIX, fig. 1) and many other Anisoptera, in which, however, it is, as a rule, imperfectly developed or not developed at all; and again in *Philoganga montana* (fig. 44). The bridge itself seems to be still extending proximally in some Lestinæ (Plate LI, figs. 6 and 7, and LIII, fig. 1), its slender proximal end being often unattached to vein M_{1+2}.

Here we have strong side light upon the early history of that most distinctive peculiarity of dragonfly wings, the crossing of the radial

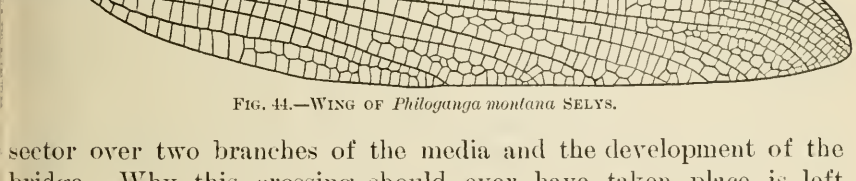


FIG. 44.—WING OF *Philoganga montana* SELYS.

sector over two branches of the media and the development of the bridge. Why this crossing should ever have taken place is left entirely unexplained. That it was established very early in the history of the group is indicated by its occurrence in very early nymphal life, crossing being no longer possible after the internal fusion of the hypoderm cells to form the tracheal channels. But, once across, it formed a weak unilateral fork upon the posterior side of vein M_2, while occupying a field where strong developments were possible. Hence a strong bridge was evolved for its support, and the development of the bridge doubtless followed the lines we have just indicated. The proximal end of the bridge in most living species joins vein M_{1-2} directly, but in most Gomphinæ it appears as if forked, and in the fossil Heterophlebinæ it joined vein M_3 directly.

In the singularly isolated fossil genus *Stenophlebia*, whose venation has been figured in a very detailed manner by Hagen,[c] there is a con-

[a] It will be remembered that the trachea *Rs* here springs directly from trachea M_{1+2}. The oblique vein (*o'*, fig. 34) marks the place of its origin; on the proximal side is the added brace (*br'*).

[b] It will be observed that this brace is better developed in the fore wing than in the hind in *Neurobasis;* similarly, the other brace just mentioned for *Chalcopteryx;* two further examples, therefore, of unequal development of fore and hind wings.

[c] Palæontographica, XV, pl. III, fig. 1.

dition of the crossing of the radial sector so curious one hesitates at attempting to explain it on the ground of published figures that were drawn without ontogeny in mind. It looks as if, a little beyond the nodus, the radial sector had crossed over but one branch of the media and had then developed a short supporting bridge; as if a stage a little less primitive than that shown for tracheæ in fig. 1, *B*, had been the permanent condition in this genus. But perhaps the interpretation of homologies given by Hagen is correct (naturally it is the only one that would occur to him), in which case the bridge is developed as a support to vein M_2, and the radial sector is shifted proximally at its base—a very curious state of things for Anisoptera! And *Stenophlebia* is distinctly anisopterous, notwithstanding its lack of differentiation between fore and hind wing. Aside from the characters just discussed, it is a very curious form in its sickle-shaped wing tips, its dislocated nodus with the subcosta descending upon the radius, its undifferentiated subtriangles, its triangles transversely placed in both fore and hind wings, and its remarkably developed trigonal supplements.

If I mistake not, it is to the readjustment of stress after the crossing of the radial sector that is due the curious bendings of veins M_3 and M_4 in many fossils (notably in *Cymatophlebia*), in some living forms of ancient aspect (*Phyllopetalia*, fig. 26, and *Chlorogomphus*, fig. 24, etc.), and in some of the more generalized members of groups at present dominant (*Gomphæschna*, Plate XXXVII, fig. 1; *Didymops*, Plate XLI, fig. 2, etc.). This bending is very different from the undulation of the radial sector in certain Libellulinæ. This is primitive, defective, and early disappears in the dominant groups, or becomes transformed into something very different and more useful. That other is recent, local, and is but one among several factors in the bracing of the wing area in which it occurs.

When vein *Cu* became unilateral on its posterior side, the weakness of this fork was corrected by the apposition of the distal end of vein A_1.[a]

It must be borne in mind that dynamic control in vein development, dynamic genesis, or whatever we call it, may be but the result of the natural elimination or subordination of those variations which do not tend toward the mechanical perfecting of the machinery of flight.

VI. SUMMARY AND CONCLUSIONS.

1. In the course of this study I have come upon numerous manifestations of developmental dynamics:

(*a*) I have shown the operation in dragon-fly wings of far-reaching

[a] This type of bracing, which is so confusing of homologies as generally to require ontogenetic study for their unraveling, is of very common occurrence near the apex of grasshopper wings.

mechanical principles, in accordance with which the potentially hexagonal areoles of the wing are arranged in the spaces they must occupy, as are other wholly unrelated potentially hexagonal structures in other organisms.

(*b*) I have shown that there is developed in this group, several times independently, a form of wing that is elsewhere most efficient—a wing broad at base and long and pointed at the apex, rigid at the front and pliant toward the rear margin—a wing combining the principle of the aeroplane with that of the scull.

(*c*) I have shown that the development of wing braces follows strictly mechanical principles, analogous braces being repeatedly developed out of homologically different parts. Many examples have been cited within the order, and one without, in the comparison of Odonate and Ascalaphid wings.

2. In this study I have indicated processes concerned with the development of these wings which will probably be found affecting the evolution of insect wings in general:

(*a*) I have shown that there are two kinds of specialization in operation throughout the order—vein shifting, concerned with securing advantageous position of the parts, and vein differentiation, concerned with the strengthening of the most important veins by an economical use of all strength-giving wing material. The former alone seems to have been made use of in venational studies hitherto; the latter is often a more sure criterion of the degree of specialization.

(*b*) I have offered a hypothetical explanation of the progressive differentiation between veins and membrane.

3. In the study of dragon-fly wing venation only the comparative anatomy of the adult wings has been drawn upon hitherto. I have added the ontogenetic method, beginning my study of the veins with that of their antecedent tracheæ. I have found this method to furnish most satisfactory evidence as to what was the primitive position of the veins in almost every part of the wing for all the principal groups of the Odonata. This, followed by careful study of adult wings, both recent and fossil, has enabled me to make some slight contributions to Odonatology proper:

(*a*) I have for the first time homologized in detail the parts of the dragonfly wing with those of the wings of insects of other orders, applying the simple Redtenbacher terminology, retaining the special terms already in use for parts not represented in other orders, simplifying some of them, and adding a few new terms for parts not hitherto designated by name.

(*b*) Homologies within the order have been pretty well understood for a long time, thanks to the labors of many able entomologists, among whom may be mentioned Hagen, Walsh, and especially that lifelong student of this order, Baron de Selys Longchamps. In 1893,

Calvert[a] critically reviewed and correctly stated the matter, adding some results of his own. I have been able to extend the study of homologies in a few parts, such as the region of the bridge, the supplements, the anal area, and several spaces in which special bracings occur. In these places occur the most distinctive venational features of the smaller groups.

(*c*) Incidentally, I have shown something of the relative values of the different characters that have been used hitherto to distinguish groups. Characters drawn from the form and position of the arculus and triangle and other strong braces have always proved reliable, but it is very clear that antenodal and other cross veins have been greatly overvalued, and it is equally clear that many other more important venational characters have not been noted. It is not the presence or absence of weak cross veins, but the position and relations of those that strongly brace the wing; not the number of rows of areoles that may fill a wide area, but the course of principal veins and of their supporting sectors, that are of first importance.

(*d*) I have been able to indicate many new minor lines of specialization within the order, and to add new and corroborative evidence to some lines already indicated by Kolbe, Karsch, and Calvert. Owing to the presence in these wings of a number of characters which may vary independently, for each of which primitive conditions are easily determined, and in each of which the several courses of specialization are easily traced, I have often been able to put forth conclusions based on the cumulative testimony of several parts. I have attempted to find such genealogic evidence as is preserved—not to create any—and have been content to drop, without any suggestion that might hinder future studies, cases in which evidence from wings alone seemed insufficient. But I have not hesitated to indicate relationships when these seemed well evidenced by the facts of venation.

4. Following my morphological study of the order with a review of its members, as distributed among the several families and genera, I mention some facts which might themselves serve independently as biological indications of specialization:

(*a*) A large group of closely related species, numerically dominant in its proper range, indicates the culmination of some type of specialization. This may affect either the nymph or the adult or both.

(*b*) Small and scattered genera, which include only the more rare and delicate species, are pretty apt to be the conservators of numerous generalized characters. However, since development has not stood still with any species, certain marks of specialization will also always appear.

[a] Trans. Amer. Ent. Soc., XX, pp. 162–169. The papers therein discussed, together with the few referred to in footnotes to these pages, constitute the whole of the useful literature of Odonate venation, hence no bibliographic list is hereto appended.

(*c*) Set apart from any group its dominant forms and there will remain those members of it which most closely ally the group with its neighbors.

5. What of genealogies based on external characters?

In this paper we have been dealing almost entirely with external characters—superficial characters, viewed from the standpoint of the physiologist. But hard parts, though dead, are the enduring mold in which the living being is cast, and represent the outcome of its struggle with environment. Therefore we may make more use of the principle of natural selection than is usually possible in the ordinary morphological work, having frequent recourse to the almost axiomatic principle that "useful structures once acquired will not be lost (other things being equal) in a single series, unless replaced by more advantageous structures." This is but a partial paraphrase of the more usual statement of the principle of natural selection, which may itself be condensed into three words—utility determines survival.

In order to apply this principle, we have, therefore, to know that the structures whose development we are tracing are useful structures. The proof of their utility may be derived from various sources. Take, for illustration, the brace to the stigma, which, we have seen, is developed from an ordinary cross vein:

(*a*) Its efficiency may be demonstrated mechanically. This I have not done, though it would not be difficult.

(*b*) It may be demonstrated experimentally. This I have done (on Agrioninæ) by cutting out a little piece of the brace in each wing and noting the resulting weakening of flight.

(*c*) It is demonstrated biologically by the success in life of those forms which possess the brace. They are the dominant members of their respective groups, being in numbers of species and of individuals vastly in the majority. With creatures absolutely dependent on their wings in mating, in feeding, and in escaping their enemies, this is ample demonstration of the efficiency of the wings as a whole, and, incidentally, of each part that is found here better developed than in the less successful members of the series. While this proof is less specific, while one may not learn from it the contribution any one structure has made to the excellence of the wing as a whole, it is the real proof after all.

(*d*) I ask no better proof of the efficiency of any structure than is furnished by its repeated independent development in those forms which are acknowledged to be the most specialized members of the several groups.

By these means we may arrive at some knowledge of the efficiency even of structures about whose use we know so little as we do of the several parts of the insect's wing.

The application of the principle above stated furnishes the means

for critical determination of the course of specialization. For instance, forms with unbraced stigma are not to be derived directly from other forms which have the stigma braced; and so for every other useful structure; and so for every stage in the development of each. When the records of the several parts (or of the several organs) agree, the arrangement of forms is simple enough. When they conflict—when one form is specialized in this character and the other in that—we are dealing with different lines of development, and the group is to be divided on the most ancient or fundamental character concerned. When a number of characters in disagreement seem of equal importance, with no preponderance of evidence in favor of any one as a basis for a first division, only a tentative arrangement of the groups, subject to change after study of other parts (or organs), is possible. Even when a number of characters are studied and all are in accord, and a small group may be arranged with confidence, evidence from additional parts or organs may show the group to be somewhat less homogeneous than it at first appeared. It is obvious that in a genealogic study that organ or part is most valuable which possesses the largest number of characters of which one may be sure he knows both primitive form and secondary conditions and characters, which may vary independently.

It is probable that every single functional organ exhibits developmental features that are characteristic of even the smallest groups, and that the true record of relationships is preserved in every organ if we could but read it. While a classification based upon a single organ is necessarily incomplete, the necessity for the incompleteness arises out of our inability to interpret or even to see the significant features. While a classification based on one organ is necessarily incomplete, it is not necessarily incorrect. It will at least be self-evident that the classification which must prevail because it expresses the concurrent record of all the parts will be hastened by the serious and careful study of each character singly, to determine the facts of its origin, development, and utility, and to trace these facts to their logical and necessary conclusions.

6. This is only a beginning of what should be done in the study of the venation of the order. The distinctive group characters need to be known, not for whole wings alone, but for every part of the wings. The results worked out in this paper are not specific enough to meet at least three immediate, practical needs. It is frequently necessary to determine fragments of wings:

(*a*) In food studies.

(*b*) In the study of unknown nymphs, whose developing wings contain the full outline of the venation of the imago. Such wings are often imperfectly preserved and are to be removed only in fragments. Their correct determination makes the most exacting demands on one's knowledge of venation.

(*c*) In the study of fossils, that are oftener fragmentary than otherwise and that present no other characters so well preserved. From the standpoint of pure science, the need of better knowledge is greatest here. The present systematic arrangement of the known fossil Odonata is a miserable jumble, and some statements that have been drawn from it in a number of books and papers on geographic distribution are quite misleading. Instances have already been cited of fossil forms that are referred to the wrong suborder. There have been some greater and many lesser unnecessary errors of reference. *Libellulium kaupii* Westwood is probably not a dragonfly at all, while *Hemeroboides giganteus* Buckman is a dragonfly of the subfamily *Isophlebinæ* (as may be seen by comparing Buckman's figure with the forewing of fig. 31), and not a huge hemerobian, as has been supposed. *Libellulium agrias* Westwood belongs in the Æschnidæ, being in every detail that Westwood figured diametrically opposed to Libellulidæ. *Libellulium antiquum* Brodie belongs in the Æschnidiinæ, and so also does the *Æschna flindersiensis* Woodward. The only fossil Æschna that seems to fit that name in the modern sense of it is *Æ. solida* Scudder. *Æschna separata* Scudder and *Æschna metis* Heer, especially the latter, which was improperly removed to *Anax* by Hagen, will go in *Hoplonæschna*. *Æschna perampla* Brodie and *Æschna hageni* Heer, judged by poor figures, will hardly go in the Æschninæ. *Stenogomphus carletoni* Scudder,[a] which was independently determined by the two most distinguished students of the Odonata, de Selys and Hagen, to be nearest *Gomphoides stigmatus* (Plate XXXIII, fig. 2) among living forms, and which stands as the only known American fossil Gomphine, is in fact a Libellulid in every line, and had the hind wing been preserved no one would have thought it a Gomphine.

While it would be manifestly impossible, owing to defective preservation, to refer fossils, in most cases, to genera of such thin cleavage as modern practice allows for recent species, it is very obvious that a new study of the types of the older authors would help much toward a better arrangement of our system. New figures of these are especially needed. Mr. Scudder's figures are the only ones that I have found entirely reliable. All others show omissions or alterations of unnoticed characters of critical importance. For instance, the oblique vein, even in Hagen's drawings, is rarely shown. This is not surprising, so long as it was regarded merely as one of a row of cross veins; but it is disconcerting in a study made from the ontogenetic standpoint. When the structural characters that are actually preserved by fossils already in collections have been fully interpreted, we shall know much more concerning the history of the group. Generalisations can not safely proceed faster than the development of real knowledge.

[a] Bull. 93, U. S. Geol. Surv., pp. 12–15, pl. 1, fig. 1.

EXPLANATION OF PLATES.

PLATE XXXI. Nymphal wings (photomicrographs).

Fig. 1. Wings of *Gomphus descriptus* Banks, nymph full grown.
2. Wing of *Lestes rectangularis* Say, grown nymph, showing the radial sector attached to the median trachea.
3. Portion of hind wing of young nymph of *Anax junius* Drury, previous to the development of any veins, showing the first indications of bridge, triangle and anal loop.

PLATE XXXII. Nymphal wings (photomicrographs).

Fig. 1. Small portion of wing of a nearly grown nymph of *Anax junius* Drury, with veins developing, showing the formation of the radial supplement (*R. suppl.*) and of the brace vein between veins M_3 and M_4.
2. The basal part of the fore wing of a nymph of *Lanthus parvulus* Selys, showing the formation of the arculus and the triangles.
3. The nodal region of the same wing, showing the formation of the bridge and the oblique vein.

PLATE XXXIII.

Fig. 1. Wings of *Gomphus dilatatus* Rambur.
2. Wings of *Gomphoides stigmatus* Say.
3. Wings of *Aphylla producta* Selys.

PLATE XXXIV.

Fig. 1. Wings of *Cyclophylla diphylla* Selys.
2. Wings of *Progomphus obscurus* Rambur.
3. Wings of *Gomphidia* sp?

PLATE XXXV.

Fig. 1. Wings of *Gomphus vulgatissimus* Linnæus.
2. Wings of *Hemigomphus ochraceus* Selys.
3. Wings of *Lanthus parvulus* Selys.

PLATE XXXVI.

Fig. 1. Wings of *Tachopteryx thoreyi* Selys.
2. Wings of *Ulula sp?* (from Brazil).
3. Hind wing of *Hemianax ephippiger* Burmeister.

PLATE XXXVII.

Fig. 1. Wings of *Gomphæschna furcillata* Say.
2. Wings of *Basiæschna janata* Say.
3. Wings of *Boyeria irene* Fonscombe.

PLATE XXXVIII.

Fig. 1. Wings of *Hoplonæschna armata* Hagen.
2. Wings of *Brachytron pratense* Müller.
3. Wings of *Æschnophlebia anisoptera* Selys.

PLATE XXXIX.

Fig. 1. Wings of *Nasiæschna pentacantha* Rambur.
2. Wings of *Staurophlebia reticulata* Burmeister.
3. Wings of *Gynacantha trifida* Rambur.

PLATE XL.

Fig. 1. Wings of *Æschna californica* Calvert.
2. Wings of *Æschna ingens* Rambur.
3. Wings of *Anax junius* Drury.

PLATE XLI.

Fig. 1. Wings of *Synthemis brevistyla* Selys.
2. Wings of *Didymops transversa* Say.
3. Wings of *Palaophlebia superstes* Selys, female.

PLATE XLII.

Fig. 1. Wings of *Neocordulia androgynis* Selys.
2. Wings of *Oxygastra curtisii* Dale.
3. Wings of *Hemicordulia tau* Selys.

PLATE XLIII.

Fig. 1. Wings of *Gomphomacromia paradoxa* Brauer.
2. Wings of *Nannothemis bella* Uhler.
3. Wings of *Perithemis domitia* Drury.

PLATE XLIV.

Fig. 1. Wings of *Agrionoptera insignis* Rambur.
2. Wings of *Anatya guttata* Erichson.
3. Wings of *Raphismia bispina* Hagen.

PLATE XLV.

Fig. 1. Wings of *Pseudophlebia minima* Kirby.
2. Wings of *Diplacodes parvula* Rambur.
3. Wings of *Mesothemis simplicicollis* Say.

PLATE XLVI.

Fig. 1. Wings of *Macrothemis celeno* Selys.
2. Wings of *Celithemis eponina* Drury.
3. Wings of *Leucorhinia intacta* Hagen.

PLATE XLVII.

Fig. 1. Wings of *Pachydiplax longipennis* Burmeister.
2. Wings of *Ephidatia longipes* Hagen.
3. Wings of *Paltothemis lineatipes* Karsch.

PLATE XLVIII.

Fig. 1. Wings of *Orthemis ferruginea* Fabricius.
2. Wings of *Belonia uniformis* Kirby.
3. Wings of *Libellula pulchella* Drury.

PLATE XLIX.

Fig. 1. Wings of *Schizopyga luctifera* Selys.
2. Wings of *Tauriphila iphigenia* Hagen.
3. Wings of *Tramea onusta* Hagen.

PLATE L.

Fig. 1. Wings of *Trithemis* sp?
2. Wings of *Uracis* sp?
3. Wings of *Pantala flavescens* Fabricius.

PLATE LI.

Fig. 1. Wings of *Pseudophæa ochracea* Selys.
2. Wing of *Epallage fatima* Charpentier.
3. Wings of *Cyanocharis ralga* Needham.
4. Wing of *Heterina* sp? (from Brazil).
5. Wing of *Rhinocypha trifasciata?* Selys.
6. Wing of *Archilestes grandis* Rambur.
7. Wing of *Megalestes major* Selys.
8. Wing of *Mecistogaster lucretia* Drury.

PLATE LII.

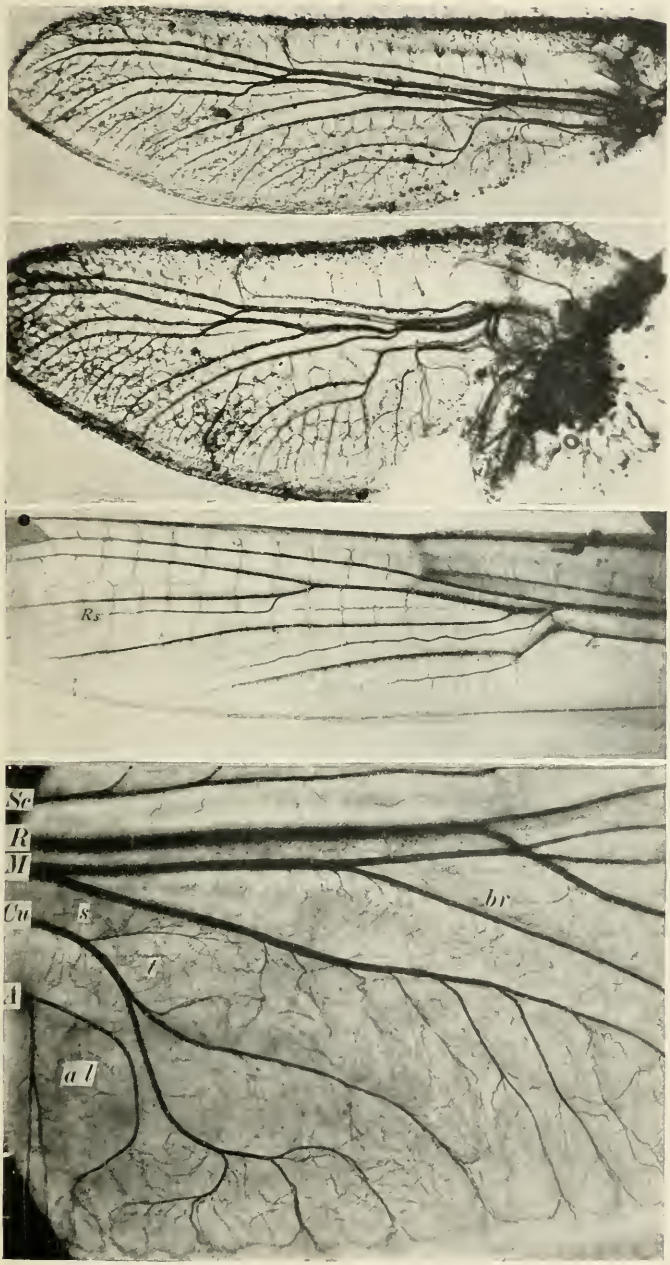
Fig. 1. Wing of *Micromerus blandus* Selys.
2. Wing of *Libellago caligata* Selys.
3. Wing of *Pseudophæa* sp?
4. Wing of *Epallage fatima* Charpentier.
5. Wing of *Rhinocypha* sp?

PLATE LIII.

Fig. 1. Wing of *Lestes tricolor* Erichson.
2. Wing of *Palæmna sp?* (from Trinidad).
3. Wing of *Platysticta maculata* Selys.
4. Wing of *Philogenia* sp?
5. Wing of *Argia fumipennis* Burmeister.
6. Wing of *Heteragrion flavorittatum* Selys.
7. Wing of *Agriocnemis pulverulans* Selys.
8. Wing of *Amphipteryx agrioides* Selys.

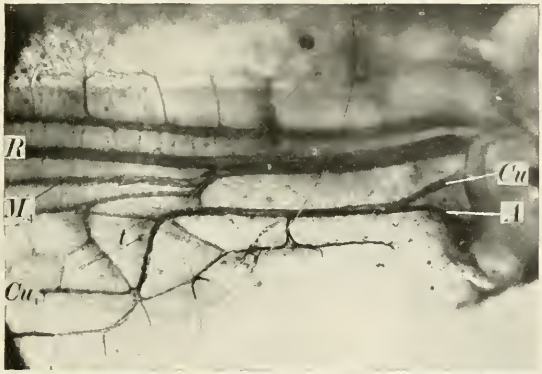
PLATE LIV.

Fig. 1. Wing of *Tatocnemis malgassica* Kirby.
2. Wing of *Disparoneura* sp?
3. Wing of *Idioneura ancilla* Selys.
4. Wing of *Cœnoneura carnatica* Selys.
5. Wing of *Hesperagrion heterodoxum* Selys.
6. Wing of *Enallagma annexum* Hagen.
7. Wing of *Erythragrion salvum* Hagen.
8. Wing of *Nehallennia irene* Hagen.



DRAGON-FLY WING VENATION.

FOR EXPLANATION OF PLATE SEE PAGE 762.



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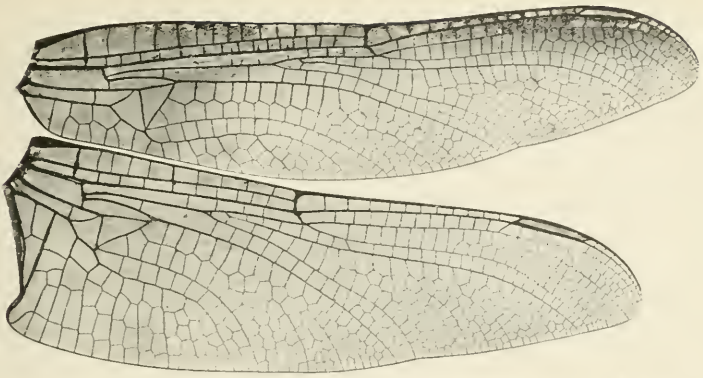

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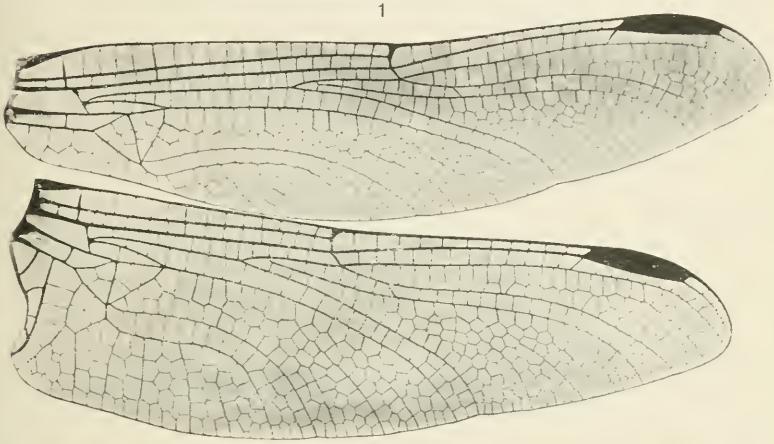

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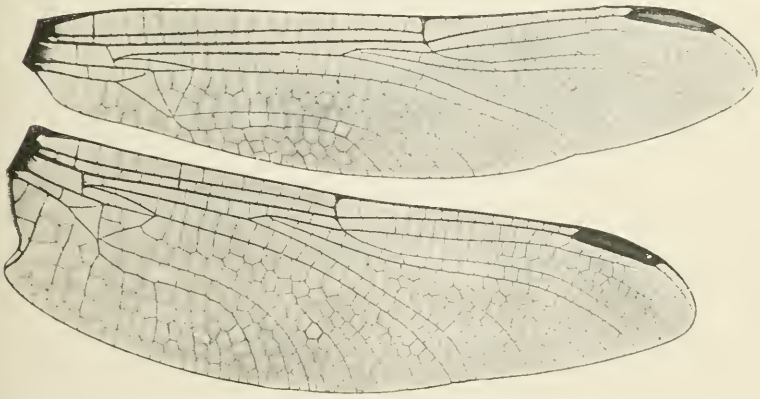

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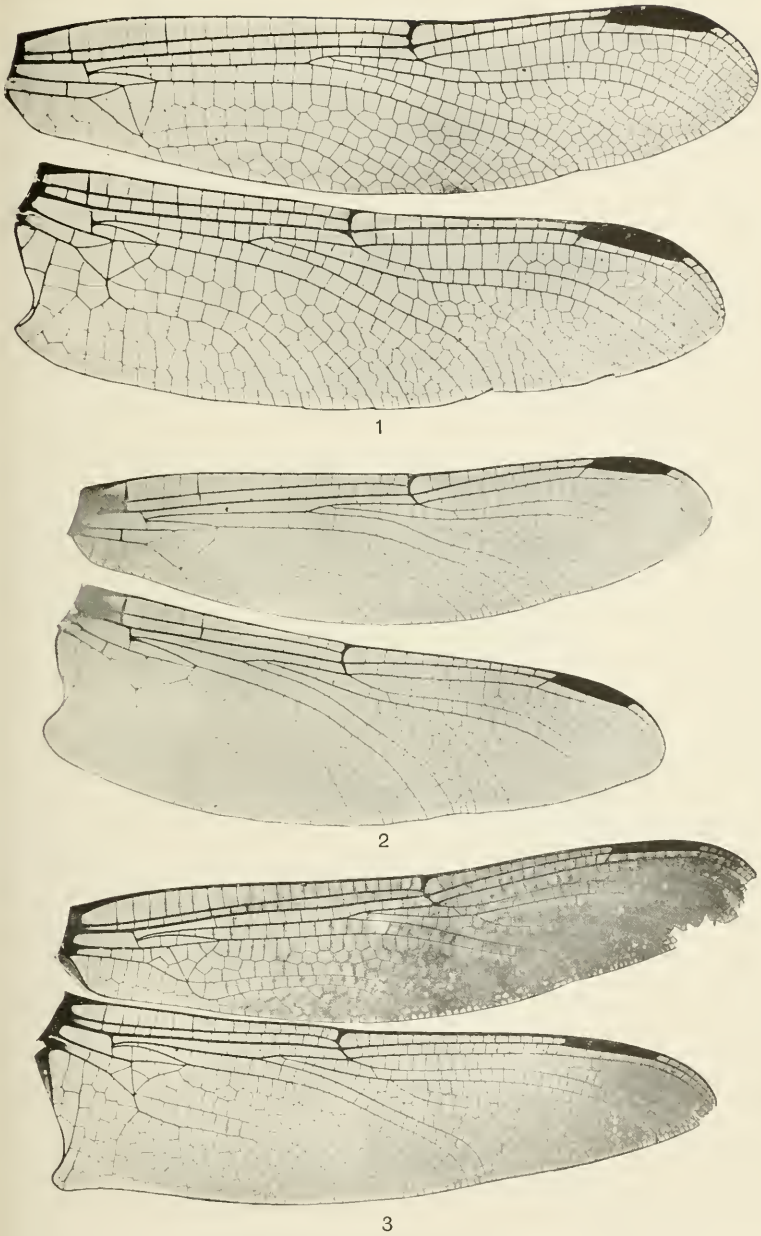

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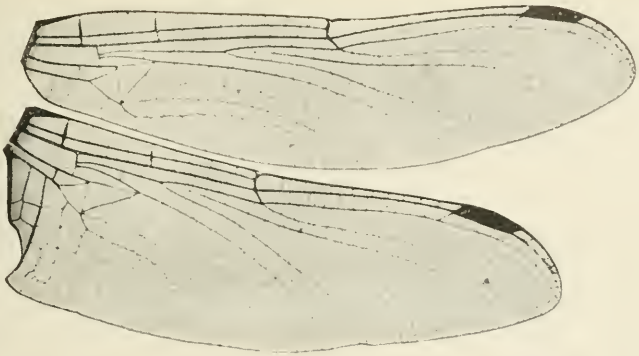

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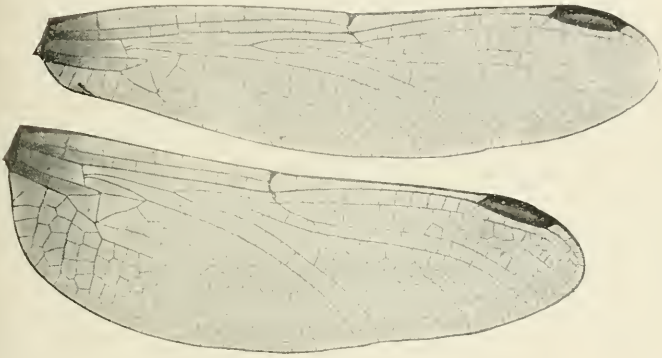

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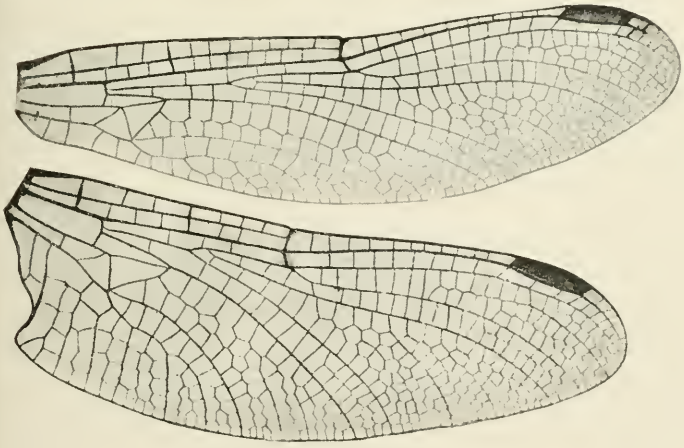

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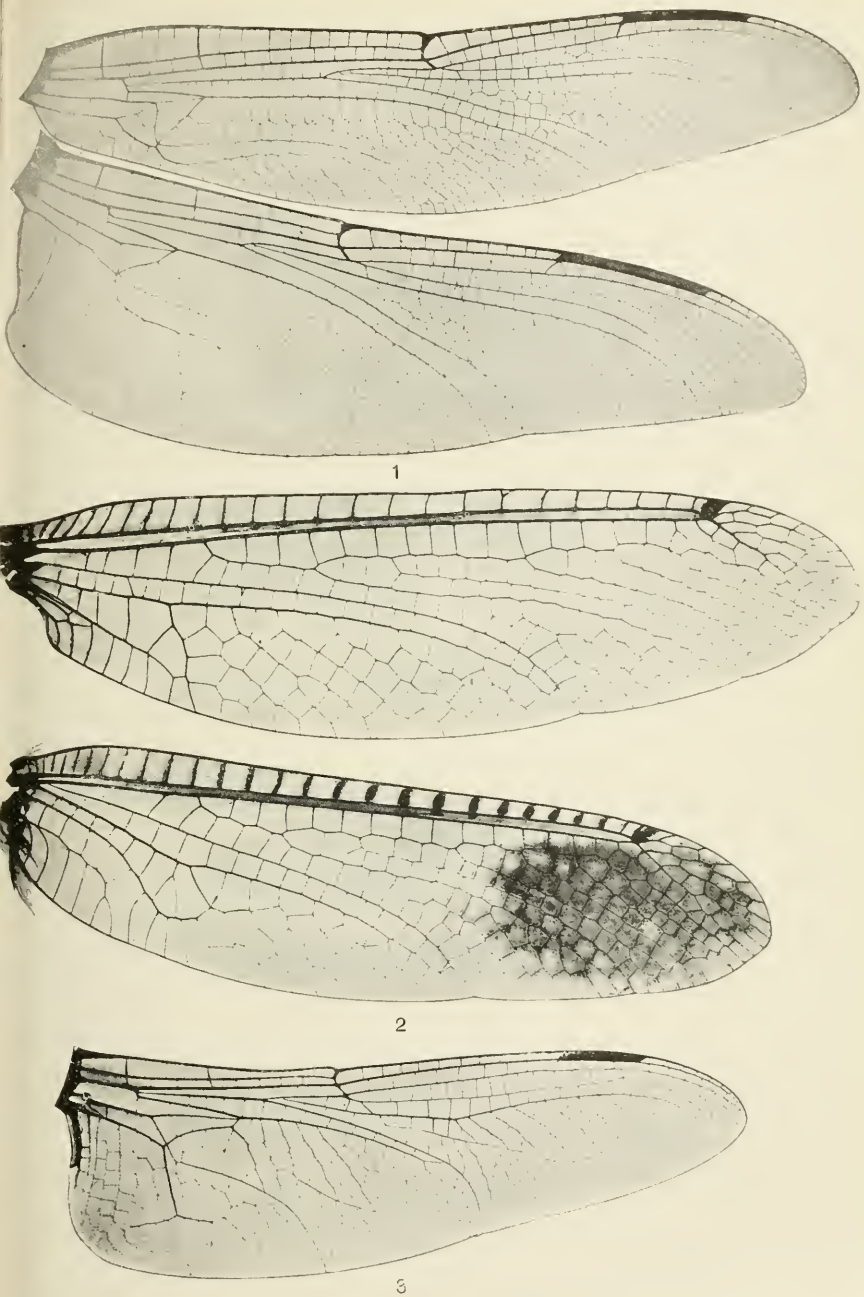

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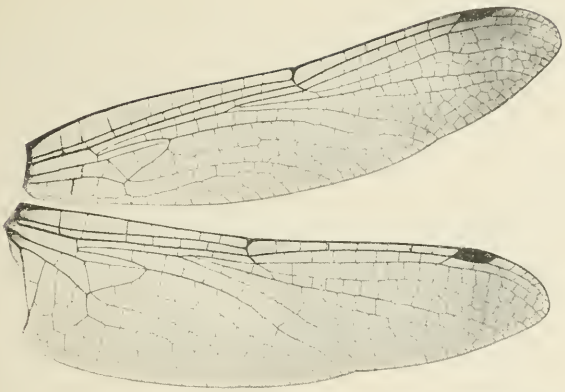

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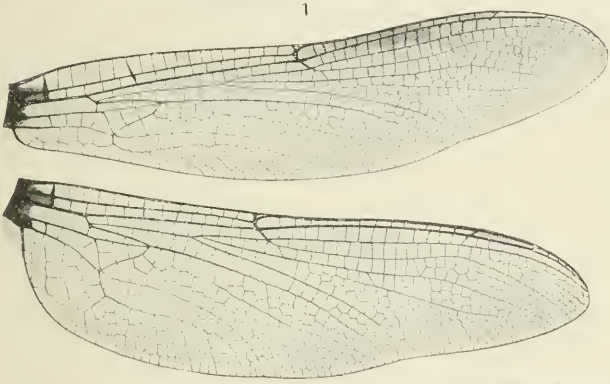

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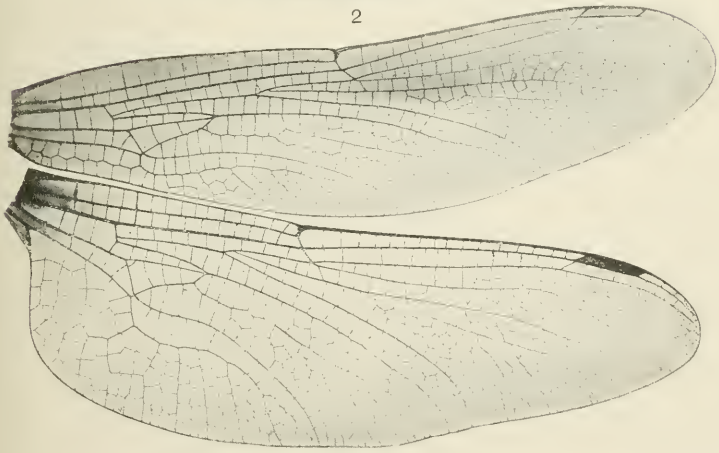

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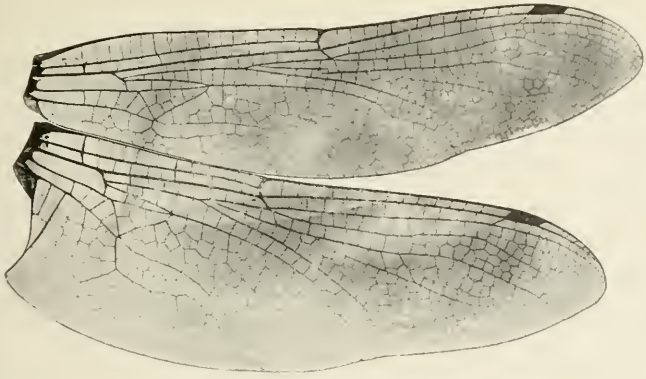

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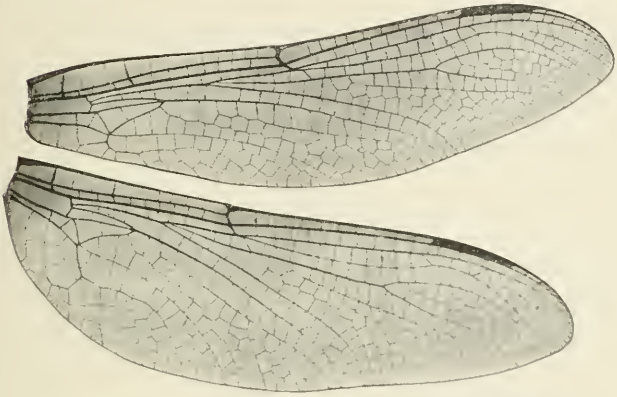

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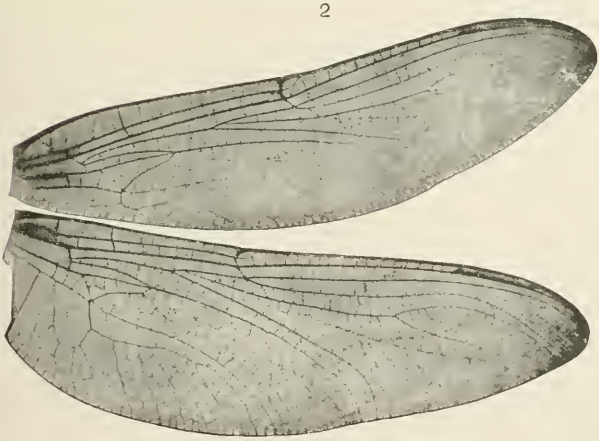

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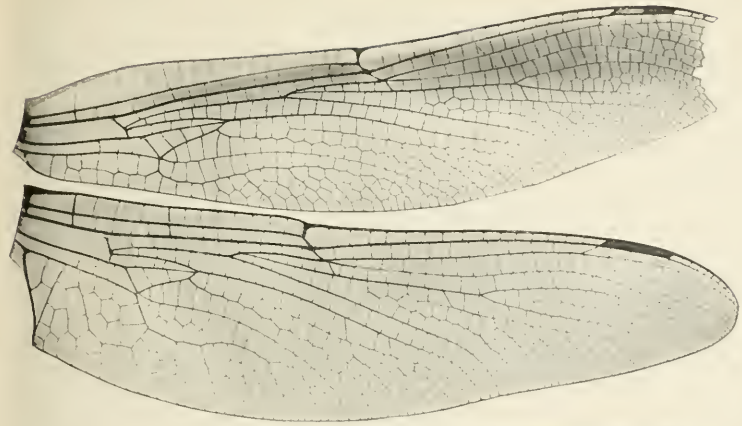

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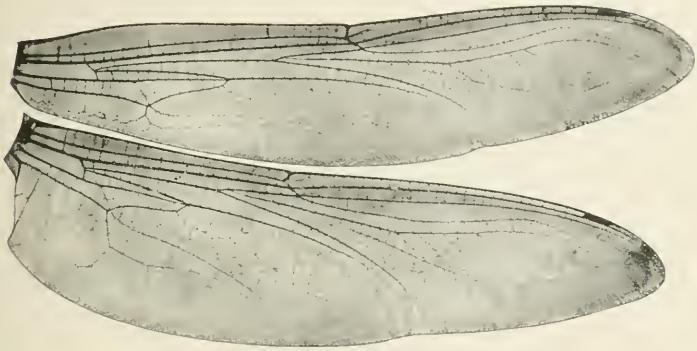

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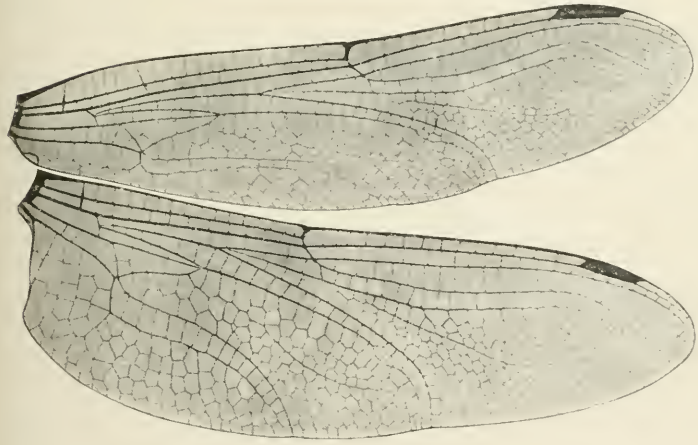

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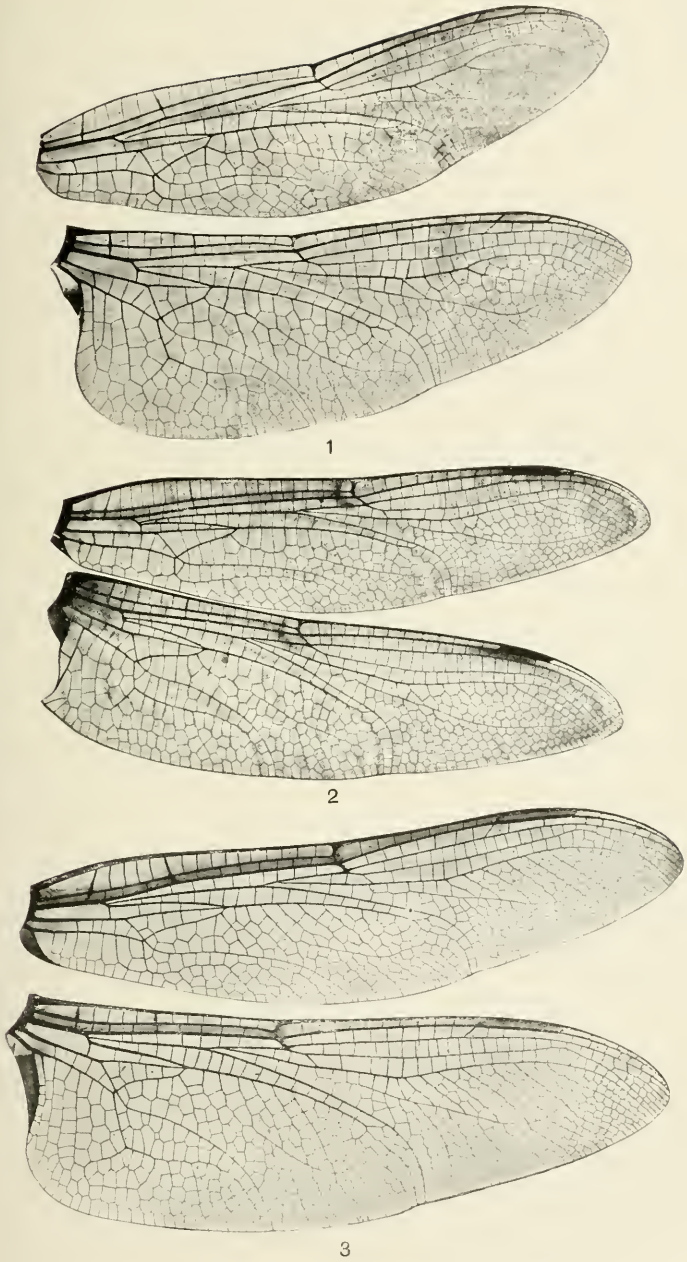

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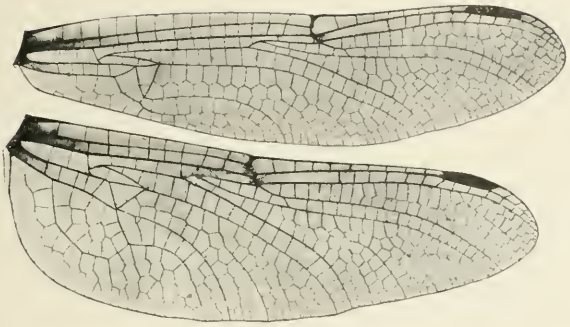

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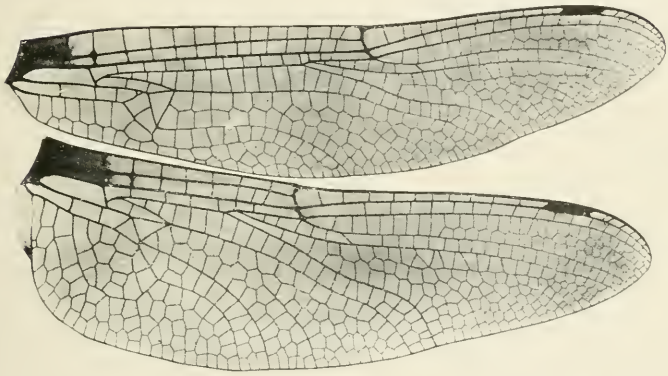

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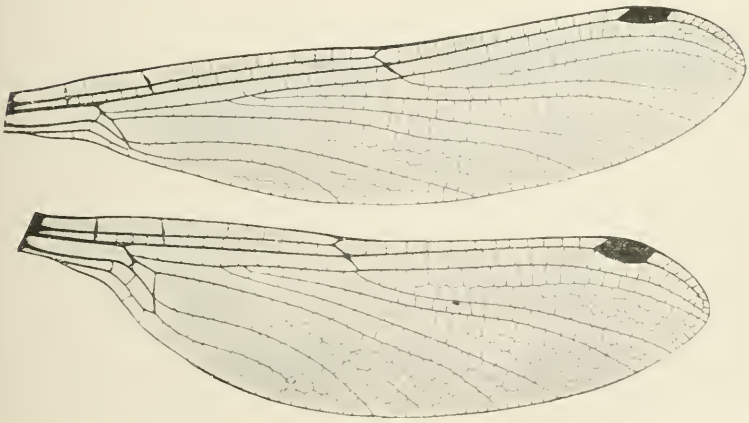

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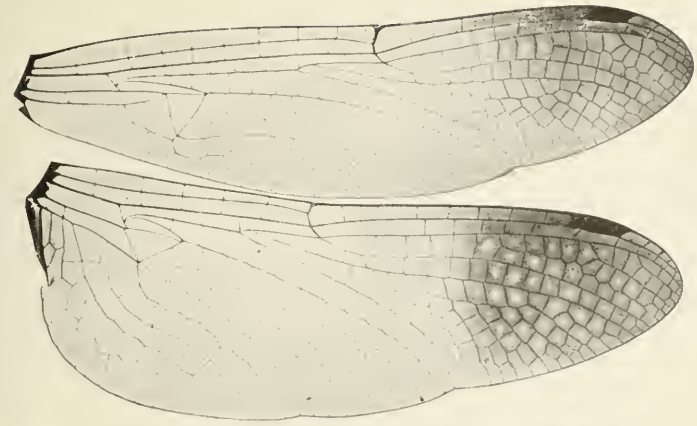

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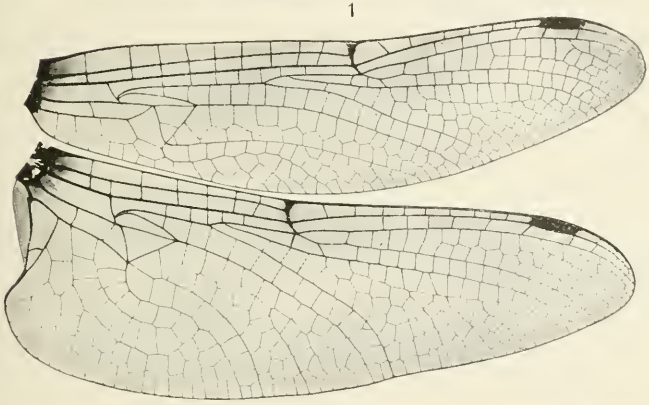

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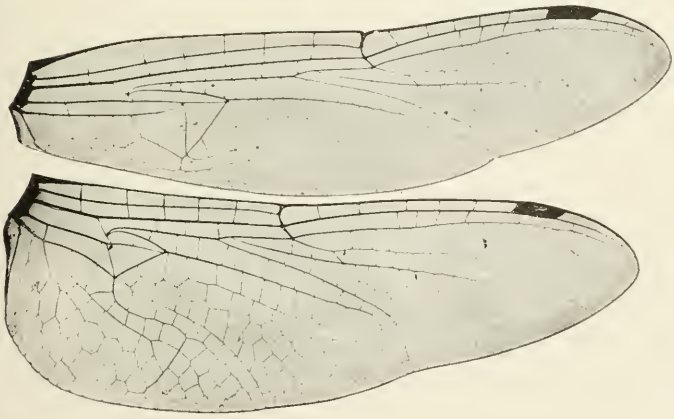

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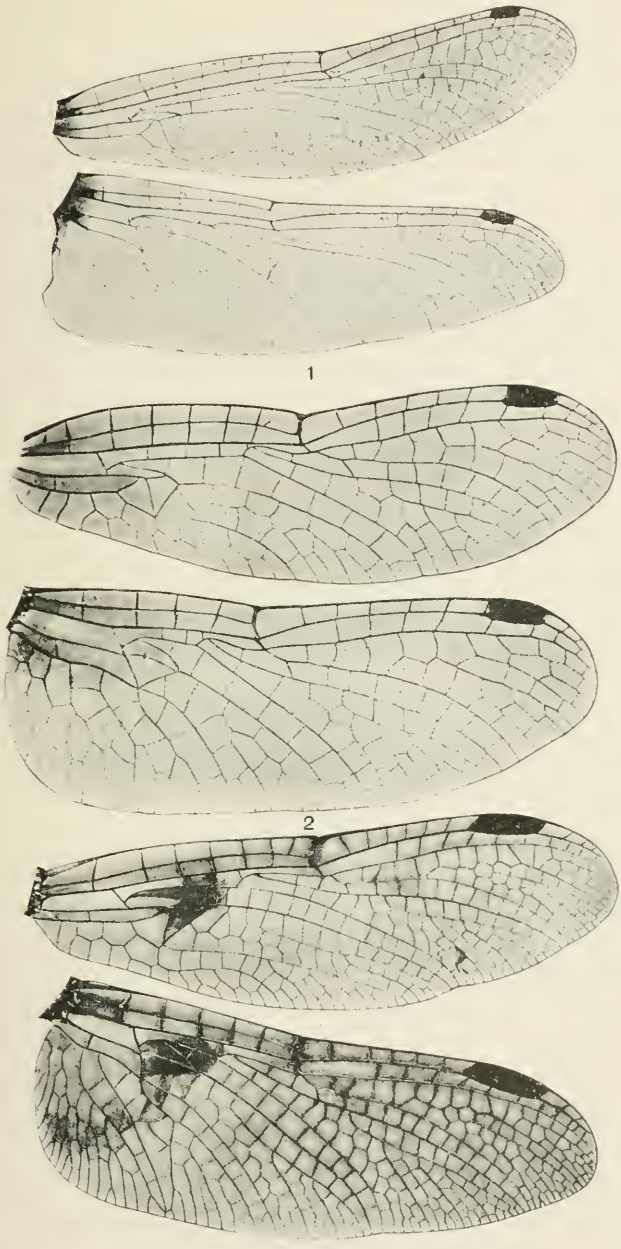

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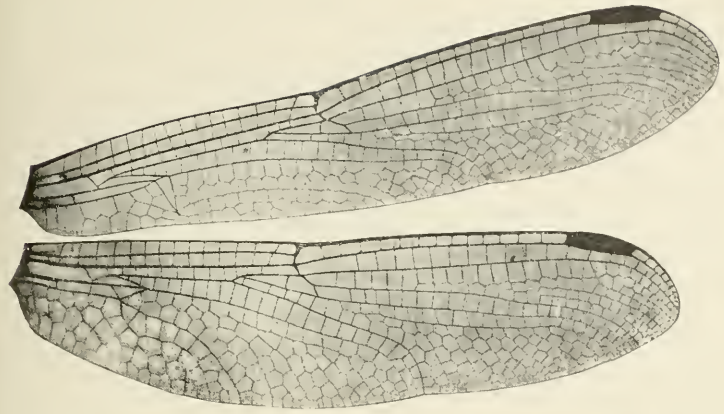

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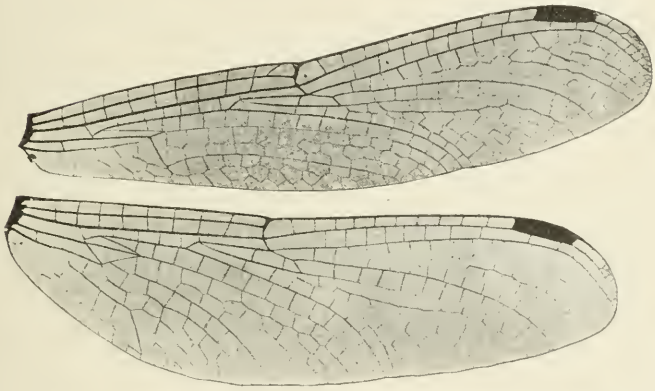

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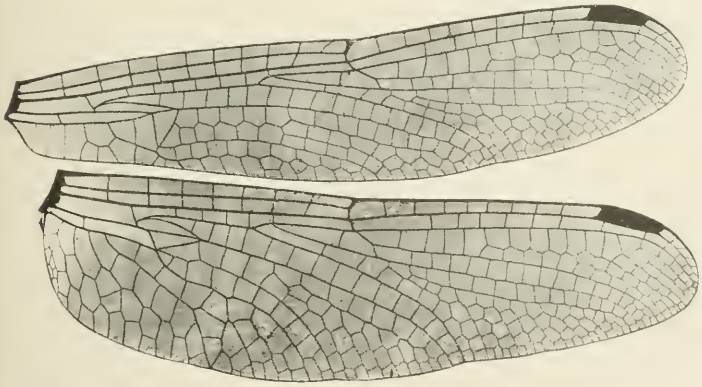

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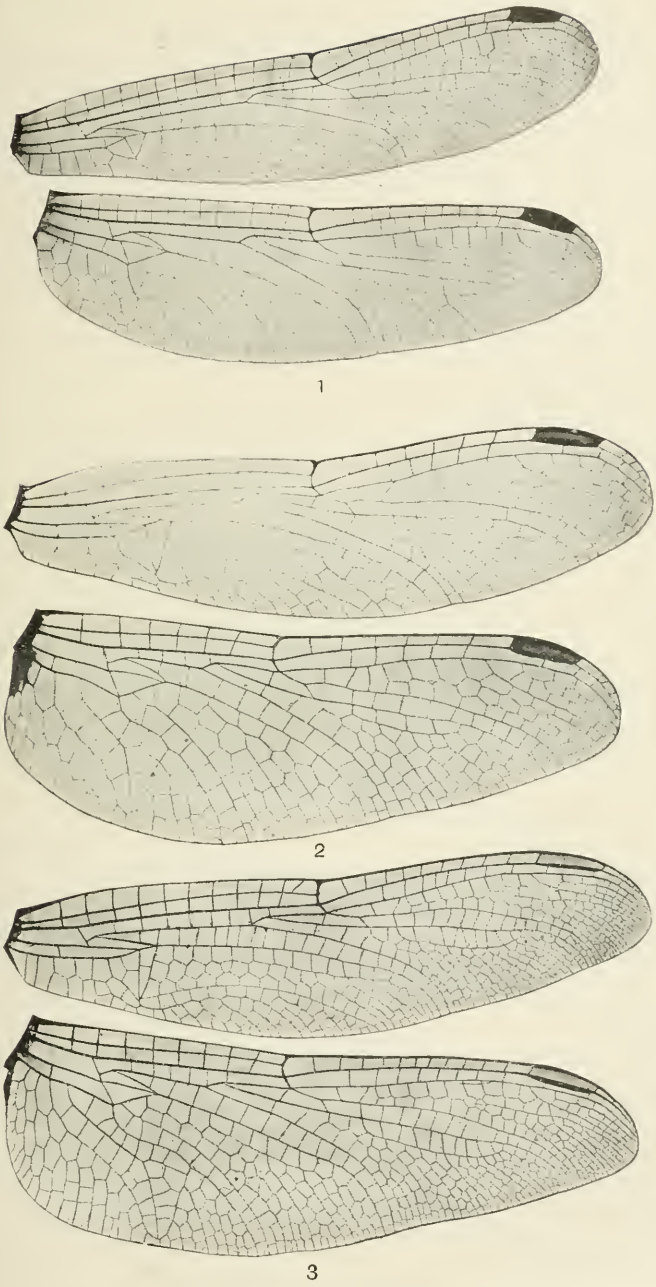

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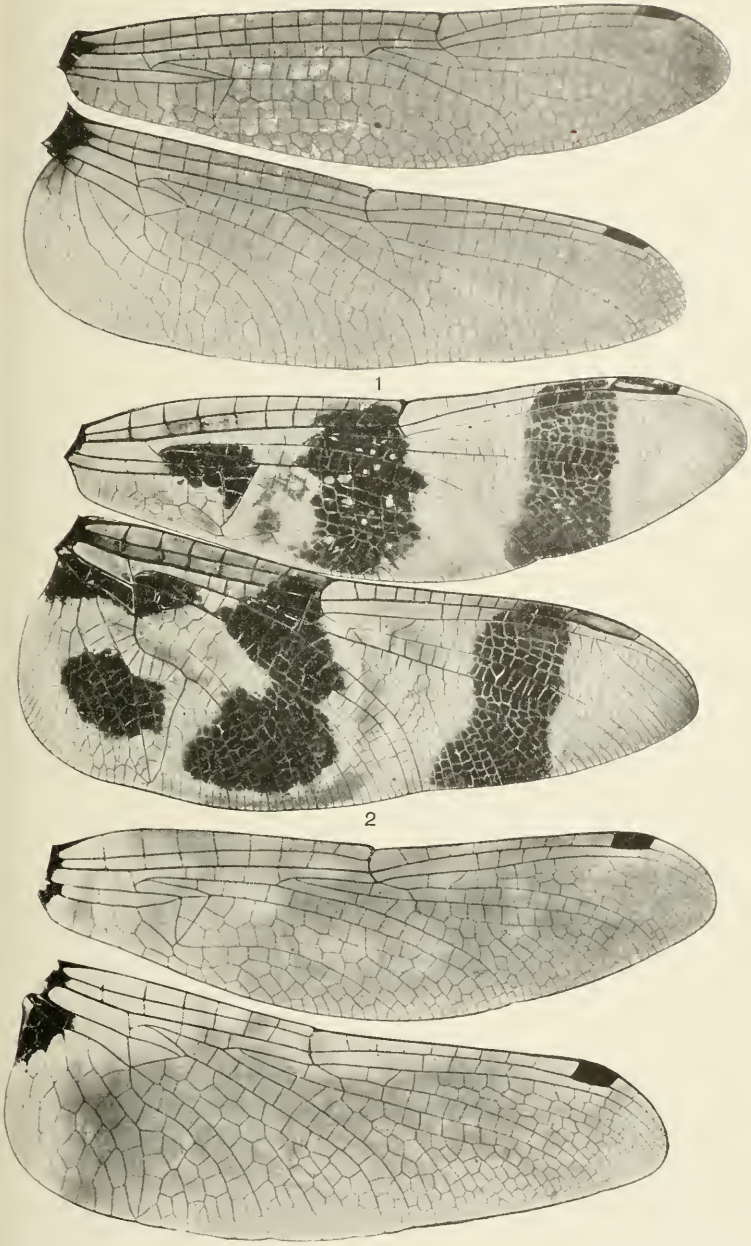

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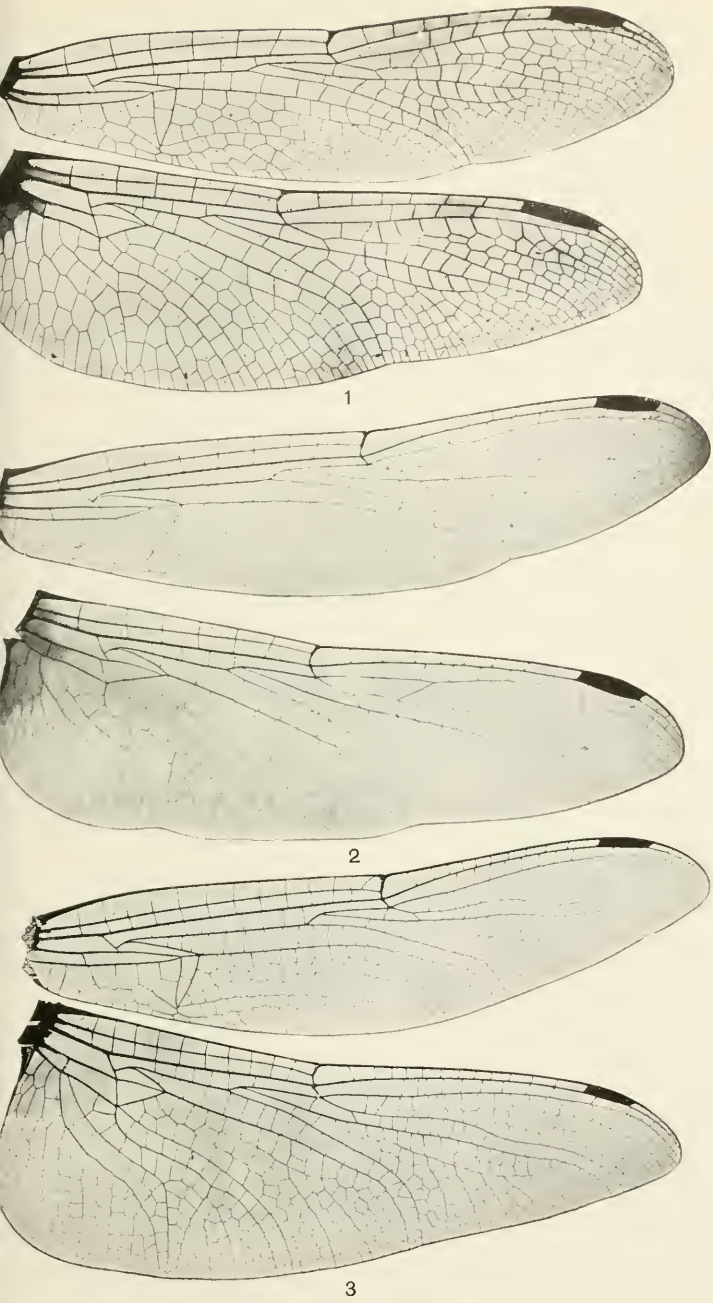

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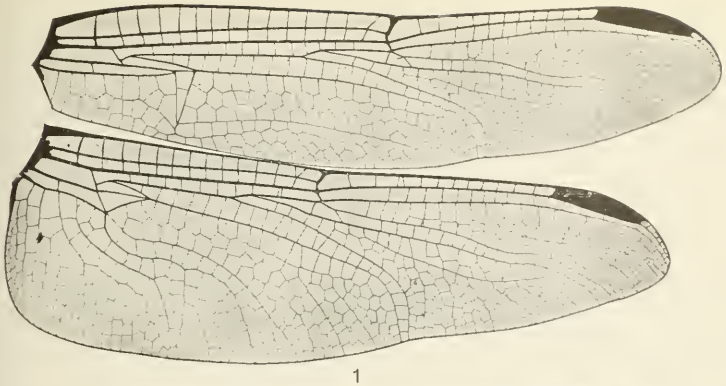

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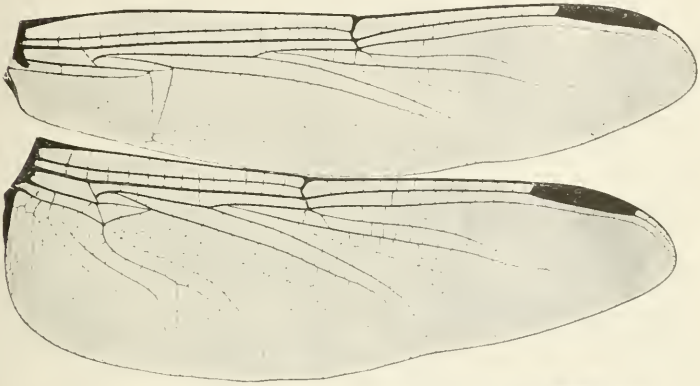

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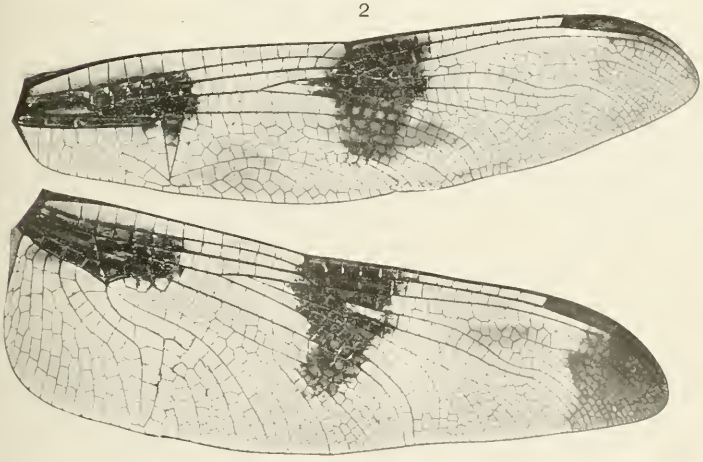

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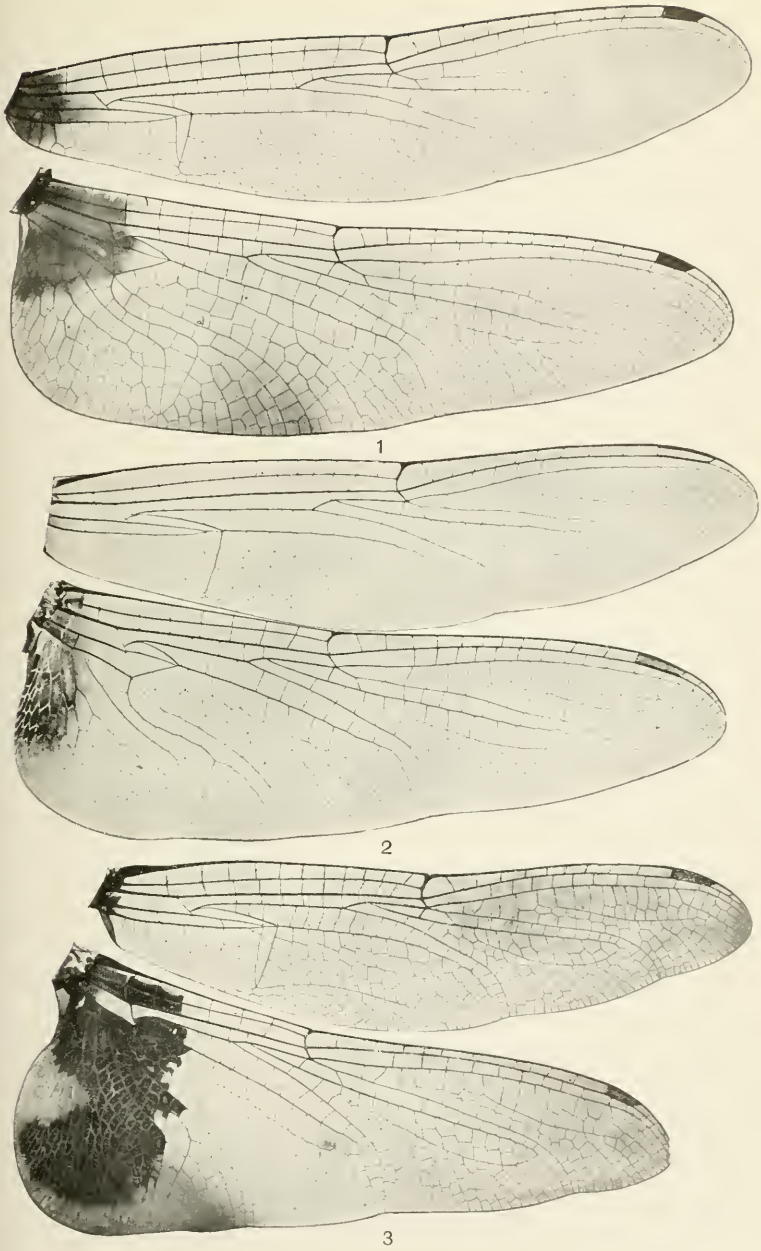
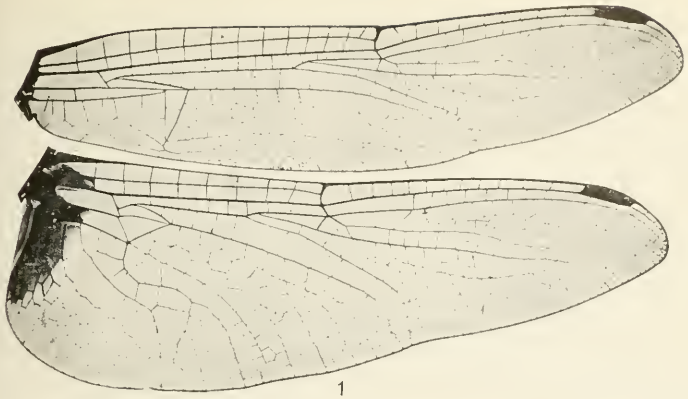
DRAGON-FLY WING VENATION.

FOR EXPLANATION OF PLATE SEE PAGE 763.



DRAGON-FLY WING VENATION.

FOR EXPLANATION OF PLATE SEE PAGE 763.



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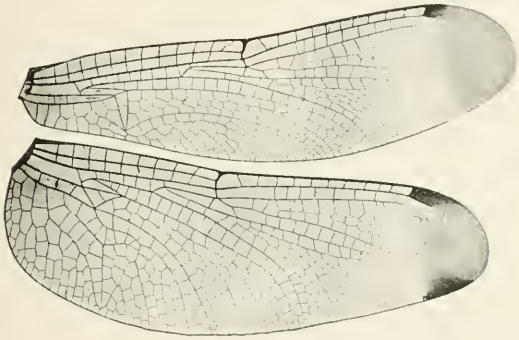

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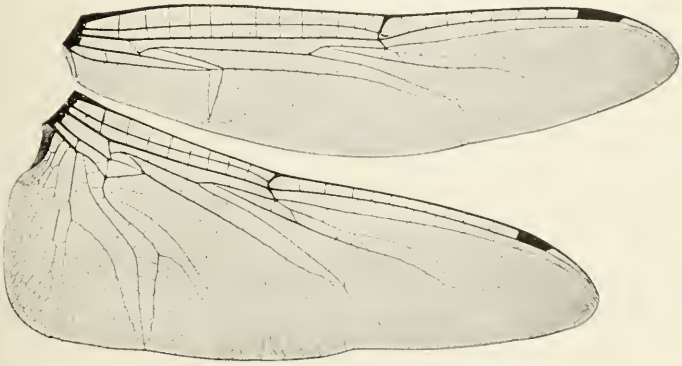

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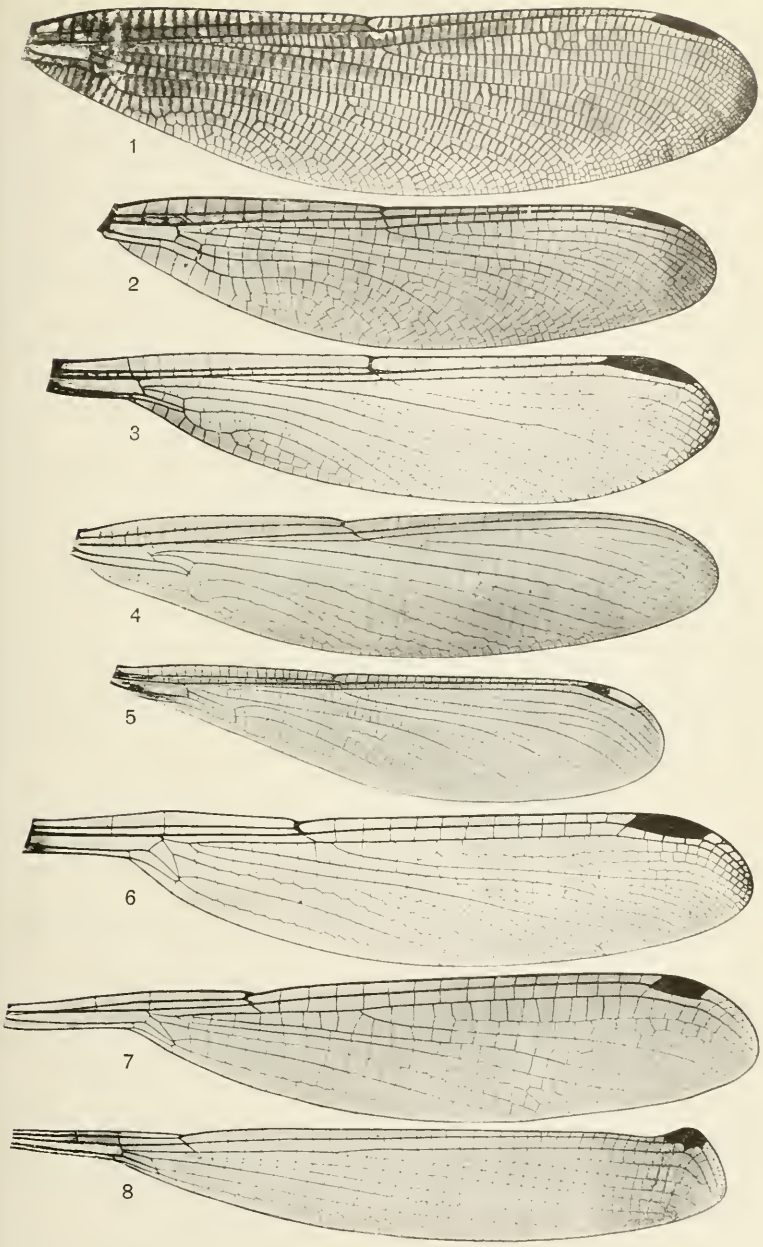
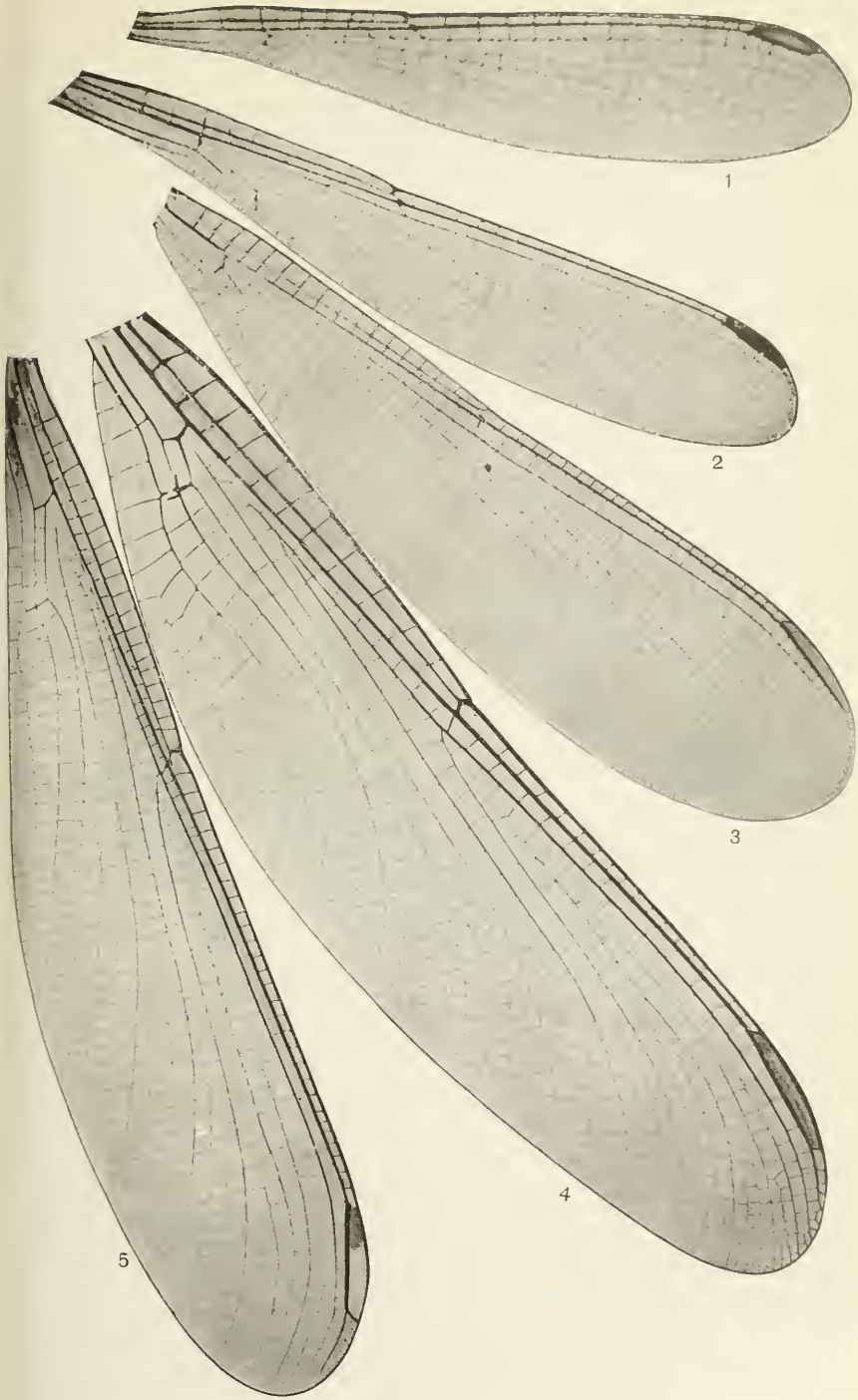
DRAGON-FLY WING VENATION.

FOR EXPLANATION OF PLATE SEE PAGE 764.



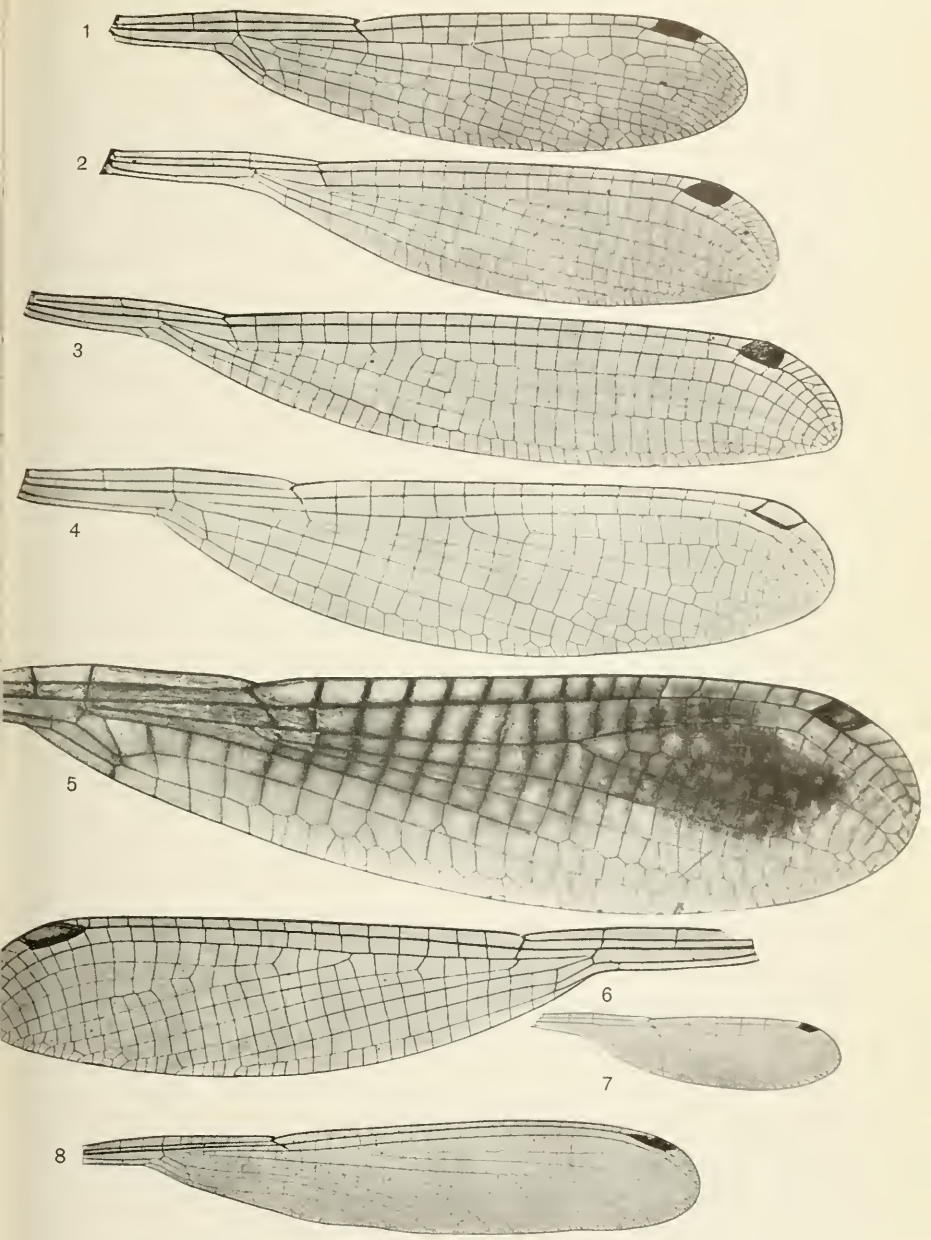
DRAGON-FLY WING VENATION.

FOR EXPLANATION OF PLATE SEE PAGE 764.



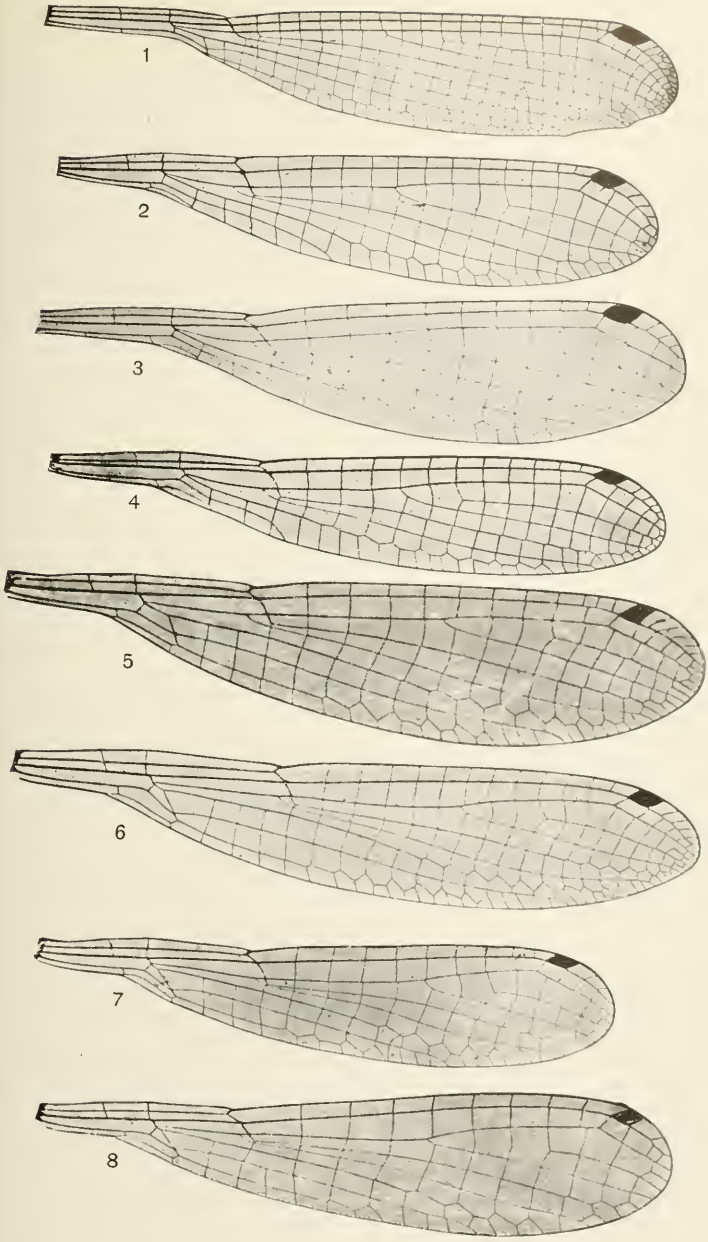
DRAGON-FLY WING VENATION.

FOR EXPLANATION OF PLATE SEE PAGE 764.



DRAGON-FLY WING VENATION.

FOR EXPLANATION OF PLATE SEE PAGE 764.



DRAGON-FLY WING VENATION.

FOR EXPLANATION OF PLATE SEE PAGE 764.