CRITICAL NOTES ON THE CLASSIFICATION OF THE CORDULIINAE (Odonata).

By James G. Needham.

Ten years ago I studied such of the dragonflies of the subfamily Corduliinae as I found accessible in this country. I made exchanges, and visited the principal museums, and was able to get acquainted with about three fourths of the known genera. I studied them especially with reference to their wings, and drew up a sketch of the principal lines of their specialization as evidenced by the wing veins. This mere outline was later included in my "Genealogic Study of Dragonfly Wing Venation".[1] There remained a number of genera of which I had no knowledge, save such as might be gained from brief descriptions, that noticed but few venational characters, and these often the least important ones. Even at so recent a date, there were no good figures of dragonfly venation published, save only a few of fossil species; and the cuts illustrating dragonfly venation in the text books were for the most part the worst of caricatures, as in some of them they still continue to be.[2]

In my first Adirondack report,[3] I attempted to arrange the North American Genera in natural order, basing the system therein used chiefly on wing venation and on nymphal characters. When characters so diverse in kind give concurrent evidence of relationships, one can arrange a group with reasonable assurance. But in my characterization of groups in that report I used beside the more fundamental characters sometimes more trivial ones, applicable only to North American genera, my object being merely to facilitate the recognition of the different members of our local fauna.

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1. Proc. U. S. Nat. Mus. Vol. 26, pp. 739–741, 1903.

2. Witness the dragonfly venation figure in Kellogg's American Insects (fig. 121, p. 89.) This is just a little better than that of stonefly venation (fig. 109) on page 73. These figures are not to be regarded bad because they are crude diagrams, but because they are false and misleading. In the diagram, for example, of the dragonfly wing (fig. 121), the arculus, the vein labelled 7 at its base and the anal veins are all shown in relations with other parts that they never bear to these parts in any living dragonfly. This is a copied figure, to be sure, and the original figures of American Insects are not subject to this criticism.

3. Bull. 47, N. Y. State Museum.

Hence, although I was able, through the tracing of lines of specialization, to indicate natural groups, I made no attempt to locate all the genera of the world in these groups, nor to set their precise boundaries.

The recent magnificent work of Monsieur R. Martin on the Corduliinae of the great de Selys collection[4] supplies excellent figures of the venation of every known genus (as well as figures of the genitalia of most of the species) and is a boon to every worker on the Odonata. Naturally, the system of classification used in this work is largely that of de Selys: but M. Martin has furnished in his illustrations and in his key abundant data for a more modern arrangement of the group. As I have had opportunity, I have been studying this data from time to time, comparing the figures with my own photographs, and drawing up a key to the genera of the world as a means of setting forth a more natural arrangement of the entire group.

I had these keys before me when Mr. Williamson's recent "Revision of the Classification[5] of the Corduliinae" came to hand, and I have studied this paper with great interest and pleasure. Williamson's arrangement of the genera is a vast improvement over the pioneer arrangement of de Selys; and the improvement grows out of better discernment as to what are the fundamental venational characters. De Selys' primary division of the group, (made, it must not be forgotten, at a time when these characters were little understood), was based upon the presence or absence of crossveins in the supertriangle. These crossveins are always weak and functionally unimportant, and if sometimes fairly constant, this is just the sort of character most likely to prove misleading at critical points. It was only by too close adherence to this criterion that Aeschnosoma, for example, could be severed from its obvious allies, Somatochlora, etc., and immolated among the coarse Macromians. Williamson abandons the use of such characters (perhaps a little too completely), and wisely bases his arrangement on the disposition of the principal veins of the wing. He arranges the genera in five groups "of approximately co-ordinate rank", and demonstrates that the members of each group possess numerous marks of affinity. But he leaves three genera *incertae sedis* (the three Corduline genera with triangles of the

4. Collections Zoologiques du Baron Edm. de Selys Longchamps; Cataloge Systematique et Descriptif. Fascicle XVII. Brussels, 1906.

5. Entom. News. Vol. 19, pp. 428–431, 1908.

fore wings four sided) out in the cold, and, quite apart from the theoretical improbability of more than two co-ordinate groups in any evolutionary series, I think he has not discriminated sufficiently as to the value of the different characters to be found in the disposition of principal veins.

Hence it will not be amiss to present in this paper some further studies on the venation of the group and their bearings on the classification.

What are the fundamental venational characters in the Corduliinae? Undoubtedly they are those connected with the differentiation between fore and hind wings. For fore and hind wing were originally alike. In each of the larger subfamilies of Odonata may be found one or more weak and dimunitive forms that have fore and hind wings much alike still. I copy Martin's figure

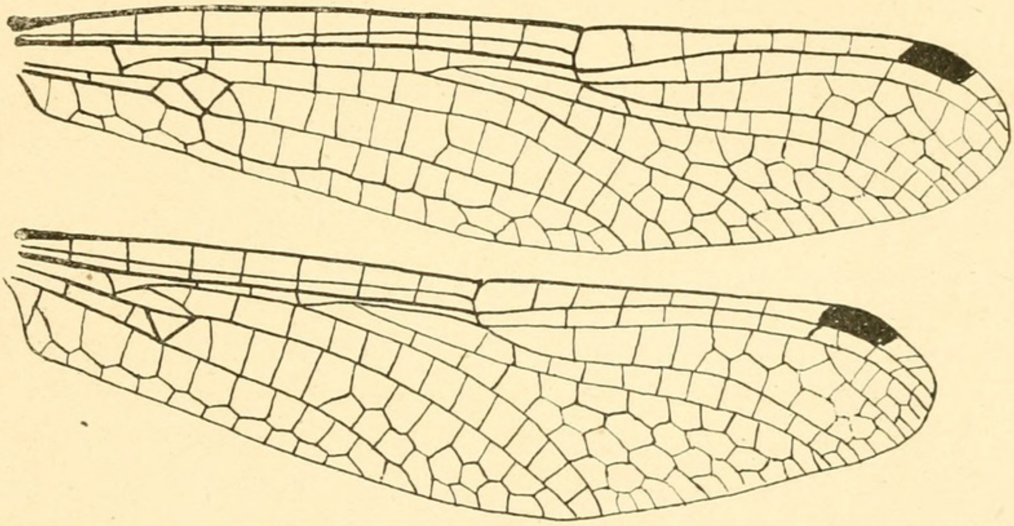

Fig. 7. The wings of Cordulephya pygmaea Selys (after Martin).

of the little Australian species, Cordulephya pygmaea Selys, in illustration of this for the Corduliinae. Here the two wings correspond with remarkable closeness, and may be compared through out, almost cell for cell. And, as were befitting in a form so generalized, the "triangle" of the forewing has not become triangular. Elsewhere[6] I have shown how the triangle is formed by the approximation of the anterior ends of two crossveins upon a neighboring vein. This process is complete in the hind wing of Cordulephya.

6. Amer. Nat. Vol. 32. pp. 903–911, 1898, and Proc. U. S. Nat. Mus., Vol. 26, p. 717, 1903.

Obviously differences in the approximation of these cross-veins are differences of degree only. Such differences are not fundamental enough for primary divisions of a subfamily. It would be hard to find three genera with less affinity than the three having four sided triangles in this subfamily. Williamson has indicated some diametrically opposite developments in Neophya and Cordulephya, and I have shown[7] that the four sided triangle of Pentathemis is not primitive, but secondarily derived from a three-sided one, and is an extreme case of specialization.

With the exception of Cordulephya, all Corduline genera have fore and hind wings of very different form. This differentiation has been brought about by a number of minor shifts of parts, which I have pointed out in the paper last cited, and *chiefly* by the broadening of the hind angle of the hind wing and the development of an anal loop for its support. This development has followed two distinct methods:

I. An anal loop of compact Cordulegasterine form (fig. 8, *d*, *l*), externally delimited by a stout straight basal segment of the vein Cu2, has interposed itself squarely between the triangle and the hind angle; and in consequence there is slight tendency for the triangle to recede to the level of the arculus. This is the group MACROMIINAE, which I characterized in 1903. It is Williamson's group V with Macromidia added. It ought to be recognizable by the characters I stated even though its constituent genera were not all named. In my judgment it is co-ordinate with all the other Corduliinae s. str. put together. If any one think it insufficiently defined, let him distinguish between the long recognized Libellulinae and Corduliinae s. str. with equal definiteness.

II. Anal loop tending from the first to be elongate and narrow and to extend itself outward along the cubital vein, with concurrent recession of the triangle to the level of the arculus (fig. 8, *a*). This is the group CORDULIINAE s. str.

These tendencies are least marked in the aberrant genera Gomphomacromia (fig. 8, *b*) and Idyonyx, in which the anal loop has remained short but even in these the form of the anal loop and its relations to the basal portion of vein Cu2, are distinct from the Macromian type: In Idionyx and in all except Gomphomacromia the bisector of the loop, dividing its two parallel rows of cells

7. Proc. U. S. Nat. Mus. Vol. 26, p. 718, footnote.

longitudinally, is established; there is nothing like a bisector in the Macromian line.

The anal loop, although just beginning to be recognized and used in the systematic study of the Odonata, has undoubtedly played a role of first importance in the evolution of the wings of the Corduliinae. Within the restricted group just defined the tip of the anal loop has developed in two divergent ways:

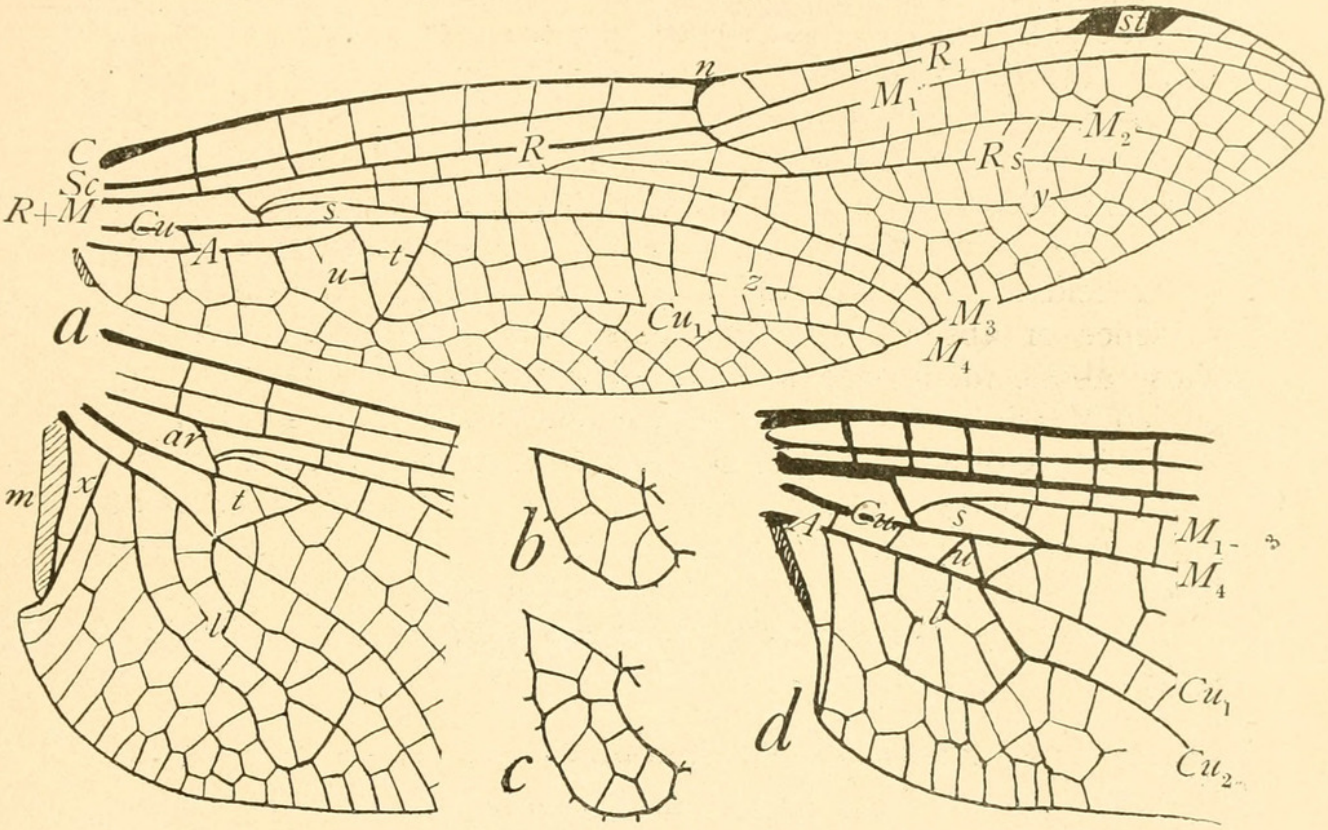

Fig. 8. Typical structures of Corduline wings: (a) the wings of Tetragoneuria cynosura Say; (b) the anal loop of Gomphomacromia paradoxa; (C) the same of Syncordulia gracilis; (d) base of hind wing of Macromia. Veins: (c), costa; (Sc) subcosta; (R) radius; (M) media; (Cu) cubitus; (A) anal; (Rs) radial sector; other branches numbered from front to rear. Other parts, (ar) arculus; (n) nodus; (st) stigma; (s) supertriangle; (t) triangle; (u) subtriangle; (m) membranule; (x) anal triangle of the male; (l) anal loop; (y) radial supplement; (z) median supplement.

(1) It has extended itself outward parallel to the vein Cu1 in a bilaterally symmetrical point, and the tendency of the triangle to be concurrently retracted to the level of the arculus has been least where the elongating loop has most closely paralleled vein Cu1. (Idomacromia, etc.) This tendency may be said to characterize in a general way Williamson's groups III and IV, with Neophya added to group IV. The Triangle has reached the level

of the arculus only in Neophya and certain species of Neocordulia, and in the latter, the anal loop is truncated on the tip and shows a very slight apical widening.

(2) On the other hand, the anal loop tends elsewhere to become unsymmetrical on its broadly truncated apical end, and to develop a long posterior angle toward the hind margin of the wing (fig. 8, *a*, *l*). This is the most salient characteristic of Williamson's groups I and II, with Pentathemis added to group II.

In endeavoring to trace the further cleavage of these groups, I have deemed these characters of most importance: (1) the primary differentiation between fore and hind wing; (2) the manner of development of an anal loop; (3) the form of the special braces formed at arculus, triangle and stigma, and (4) the mutual adjustments of the principal branches of veins in the outer field of the wing; and I have used such characters as the presence or absence of crossveins, only when characters like those above mentioned seemed to be wanting. I have largely copied Martin's arrangement of the genera of Williamson's group I. The minor divisions of the key need to be checked by the study of other characters. The venation of the Odonata is at the present time receiving more than its share of attention. There is great need of critical comparative study of other organs, and there is especial need of more knowledge of the immature stages.

KEY TO THE GENERA OF THE CORDULIINAE, s. lat., OF THE WORLD.

(Based on venational characters.)

a) Anal loop compact, little longer than broad, without bisector, delimited distally by a short straight basal segment of vein Cu2; triangle of the forewing transversely elongate, and that of the hind wing never retracted toward the arculus. SUB-FAMILY MACROMIINAE.
- b) Veins M3 and M4 straight or regularly arcuate behind the nodus.
  - c) Median (or basal) space traversed by crossveins; alternate antenodals often hypertrophied or thickened. . . . . **Synthemis**
  - cc) Median space destitute of crossveins; anal loop considerably longer (in the axis of the wing) than broad. . . . . . . **Macromidia**
- bb) Veins M3 and M4 distinctly undulate behind the nodus in both wings.
  - c) Triangles and subtriangles of the forewings traversed by crossveins.
    - d) Vein Cu where it bounds the subtriangle of the forewing on the proximal side strong and straight . . . . **Azuma**
    - dd) Vein Cu where it bounds the subtriangle of the forewing, weak and angulate among the cells. . . . . **Epophthalmia**
  - cc) Triangles and subtriangles of the forewings free from crossveins.
    - d) Triangle of the forewings followed by two rows of cells. . **Macromia**
    - dd) Triangle of the forewings followed by a single row of cells. . . . . **Phyllomacronia**

aa) Anal loop when present of elongate form bounded distally by a curving basal segment of vein Cu2, and traversed lengthwise by a more or less distinct bisector; two postanal cells in the forewing. SUB-FAMILY CORDULIINAE s. str.

b) With fore and hind wings closely similar; no anal loop. . . . **Cordulephya**

bb) Hind wings broader than the fore and with well developed anal loop.

c) Anal loop not widened at the distal end, nor with an unsymmetrical prolongation of the apex toward the hind margin. Triangle not retracted to the level of the arculus.*

d) Triangle of the forewing four sided; that of the hind wing retracted to the arculus, and the hind angle of the wing greatly expanded . . . . **Neophya**

dd) Triangle of the forewing normal; that of the hind wing not retracted to the arculus.

e) Anal vein extends almost or quite directly to the hind angle of the triangle in the forewing, and the subtriangle is elongate and four sided; veins M1–3 and M4 descend the arculus its entire length, and are fused for an equal distance beyond it in both wings; post-nodal space (space between the nodus and the stigma) but half as long as the antenodal. . . . . **Idionyx**

ee) Anal vein reaches the triangle after being twice strongly deflected around the angles or the subtriangle; subtriangle three sided; postnodal space two thirds as long as the antenodal.

f) Veins M3 and M4 parallel at their distal ends: the bisector of the anal loop divides the basal part unequally, some of the cells on the side of it next the triangle being again divided.

g) With well developed median supplement in both fore and hind wing. . . . . **Idomacromia**

gg) With no median supplement developed in either wing **Nesocordulia**

ff) Veins M3 and M4 divergent to the outer wing margin anal loop consisting of but two rows of cells about equally divided by its bisector.

g) Anal loop short, and lacking a distinct bisector. . . . . **Gomphomacromia**

gg) Anal loop longer, and with distinct bisector.

h) Veins M3 and M4 of the forewing strongly divergent at tips; bisector of the anal loop (fig. 8, *c*) weak and angulate between the cells. . . . . **Syncordulia**

hh) Veins M3 and M4 of the forewing but slightly divergent at the wing margin: bisector of the anal loop better beveloped, usually but little angulated: stigma at least three times as long as wide.

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* Except in Neophya which is specialized so independently it will cause no confusion, and in one or two species of Neocordulia, which are truly synthetic forms, but in which the anal loop is rather more squarely truncated on the ends than in any of the others. N. volxemi Sel., in my opinion, agrees in all essential characters with typical Neocordulias, and ought not to be removed to Gomphomacromia, with which it does not at all agree in such important matters as the form and relations of the triangles the form of the anal loop, the conformation at the arculus, or the venation about the stigma.

The number of cell rows in a given wing area, like that beyond the triangle, when variable, is always determined merely by the presence or absence of weak crossveins.

Neophya is remarkable for the contrast between the two wings in point of specialization. The forewing has a triangle of the most primitive sort, while the hind wing exhibits the maximum of broadening of the hind angle together with complete retraction of the triangle to the arculus.

i) Veins M1–3 and M4 separate at their departure from the arculus in the forewing . . . . **Oxygastra**
ii) Veins M1–3 and M4 fused a little way beyond the arculus in the forewing . . . . **Neocordulia**

cc) Anal loop widened at its distal end and truncated more or less unsymmetrical, the hind angle being produced sensibly toward the adjacent wing margin. Triangle of the hind wing always retracted as far as the level of the arculus.

d) Veins M1–3 and M4 fused beyond their departure from the arculus; cells along the middle of the anal loop divided by the bisector very unequally, those lying on the cubital side being much narrower. Vein M3 distinctly undulate behind the nodus; median supplement distinctly developed in the fore wing; supertriangle with crossveins.

e) Veins M1–3 and M4 fused into a straight stalk at their departure from the arculus . . . . **Pentathemis**

ee) Veins M1–3 and M4 strongly arched forward at their departure from the arculus.

f) With more than 10 antenodal crossveins: superior appendages of the male forcipate . . . . **Aeschnosoma**

ff) With 10 or fewer antenodal crossveins; appendages of the male not forcipate . . . . **Libellulosoma**

dd) Veins M1–3 and M4 not fused in the forewing at their departure from the arculus: vein M3 straight or regularly arcuate behind the nodus. Supertriangle free from crossveins.

e) Veins M4 and Cu1 divergent to the wing margin.

f) Bisector of the anal loop furcate at the slightly unsymmetrical widening of distal end . . . . **Platycodulia**

ff) Bisector of the anal loop running into the posterior prolongation of the very unsymmetrically widened distal end . . . . **Neurocordulia**

ee) Veins M4 and Cu1 not divergent to the wing margin, usually slightly convergent.

f) Hind angle of hind wing rounded in the male: vein M4 more or less broken . . . . **Hemicordulia**

ff) Hind wings angulate in the male.

g) 2nd cubito-anal crossvein present in the hind wing (therefore, the subtriangle present).

h) wings spotted . . . . **Epitheca**

hh) Wings clear . . . . **Somatochlora**

gg) 2nd cubito-anal crossvein (and therefore also the subtriangle) absent in the hind wing.

h) Triangle of the forewing traversed by a crossvein.

i) Wings spotted with brown.

j) Triangle of the hind wing traversed by a crossvein, **Epicordulia**

jj) Triangle of the hind wing open.

k) Antenodals of the hind wing 6 . . . . **Helocordulia**

kk) Antenodals of the hind wing 4 or 5 . . **Tetragoneuria**

ii) Wings clear.

j) Antenodals about equal in number to the postnodals in the forewing . . . . **Cordulia**

jj) Antenodals decidedly more numerous than the postnodals in the forewing, **Procordulia and Paracordulia**

hh) Triangle of the forewing open . . . . **Dorocordulia**