STUDIES IN AUSTRALIAN NEUROPTERA.

No. 5. The Structure of the Cubitus in the Wings of the Myrmeleontidae.


(With three Text-figures).

In No.1 of this series of Studies,* I worked out the wing-venation of Myrmeleon uniseriatus Gerst., from the pupal wing-tracheation, and showed how, in the forewing, the apparently simple vein M was in reality a forked vein, the vein usually considered to be Cu₁ being in reality the cubito-median, Cu₁ + M₂, and the point of incidence of M₂ on to the line of Cu₁ being marked by the foot of the oblique vein O. The branch descending from the point of bifurcation, which I called the cubital fork (cuf), was, naturally enough, taken to be Cu₂. It was on the lack of specialisation of this branch, that I based my argument for the recognition of the tribe Protoplectrini, of which the correct name should be Creagrini, as previously given by Navás.

In No.4 of this same series of Studies,† when describing the wing-venation of the Hemerobiidae, I showed how, in the fore-wings of Drepanepteryx and Drepanacra, an archaic Cu₂ was present close to the base, and that, in addition to this, Cu₁ was strongly branched at a sharp angle, much further distad, into two veins which I called Cu₁a and Cu₁b. In the allied genus Drepanomina, the archaic Cu₂ is lost, and replaced by a furrow. In the majority of the smaller Hemerobiidae, even the furrow has disappeared. Thus, in the most highly specialised forms of the family Hemerobiidae, all traces of the original Cu₂ are lost, and

* These Proceedings, 1915, xl., Pt.4, pp.734-751, Pl. lviii.
there is left only the distal secondary forking of Cu₁ into Cu₁ₑₐ and Cu₁ₙₙ, the point of bifurcation being properly termed the secondary cubital fork ("cnf").

Now the resemblance between the condition of the cubitus in the forewings of these smaller specialised Hemeroobiidae, and in the forewings of the Myrmelcontidae, is too striking to be ignored. It suggested to me at once that the veins which I had named Cu₁ and Cu₂ in the Myrmelcontidae were in reality only Cu₁ₐ and Cu₁ₙ, respectively, and that, if the true Cu² still existed, it must be sought for near the extreme base of the wing. I therefore examined a considerable number of Myrmelcontidae, and found that, in many cases, there could be detected, close to the base of the wing, a semi-opaque connecting-vein, not unlike an oblique vein, (though not so well defined) running across from Cu₁ to 1.A. This appeared to me to be the remains of Cu₂. With a view to proving this point, I decided to examine the pupal tracheation of some of the older Myrmelcontidae, belonging to the subfamily Dendroleontine, in the imagines of which this supposed remnant of Cu₂ appeared to be much more evident than in the genus Myrmeleon itself.

Most of the larvae of the Dendroleontine do not make pit-falls, but must be sought for either in loose sand, or in rubble or débris collected at the bases of large trees. During the winter of 1916, larvae of several genera of this type were collected around Sydney. A number of these spun up in the following September. At the end of a fortnight, three likely-looking cocoons were opened, but were found still to contain larvae. They were then placed under close observation until pupation took place. The first pupa examined proved to be very recently formed; so that, although a good dissection of the forewing was obtained, the structure was so exceedingly delicate that all the air passed out of the tracheae before either a photomicrograph or a camera-lucida drawing could be obtained. With the second dissection, I decided to take no risks, but removed it at once to the microscope-stage, and made a camera-lucida drawing of it. Both the pupal tracheation and the imaginal venation showed up very clearly, and the result was
Text-fig. 1.

Tracheation of forewing in the pupa of Xanthohon hefinsi Tillyard; (× 35).

Text-fig. 2.

Venation of Xantholeon hefinsi Tillyard; a, basal half of forewing, (× 4½); b, basal portion of same, enlarged, (× 10); c, base of hindwing, (× 4½).

LETTERING OF TEXT-FIGURES.

1A, 2A, 3A, first, second, and third analis, respectively—1A + Cu₂,

cubito-anal—C, costa—Cu, cubitus; Cu₁, Cu₂, its two principal branches; 

Cu₃, Cu₄, the two principal branches of Cu₁—Cu₄a + M₂, cubito-median—cuf, primary, and cuf′, secondary cubital fork—fr, vestigial frenulum—M, media; M₁, M₂, its two principal branches—mf, median fork—Oc, 

cubital oblique vein—Om, median oblique vein—R, radius—Rs, radial sector—rf, radial fork—Sc, subcosta.
a complete success, which is here reproduced in Text-fig. 1. As the venation was complete, and even the delicate pigmentation of the imaginal wing could be noted, I was easily able to determine this wing as belonging to the rather rare insect *Xantholeon helmsi* Tillyard,—a result as fortunate as it was unexpected, since *Xantholeon* is certainly one of the most archaic of our Australian *Myrmeleontidae*.

The result of this examination can be gathered by comparing Text-figs. 1 and 2. It will be seen that it not only bears out in full my suspicions concerning the real position of *Cu₂*, but shows also a further unexpected point of interest. For the trachea *Cu₂* is not a weak remnant descending to 1A, as the examination of the imaginal venation had led me to suspect, but is a strong trachea which has captured the line of 1A, in the same manner that *M₂* has captured the line of *Cu₁a*. In both cases, it is the upper trachea that prevails, the lower that goes under. In both cases, the crossing of the upper trachea on to the level of the lower is marked, in the imaginal venation, by an oblique vein, which represents, of course, the actual basal piece of the upper vein in question. We must therefore distinguish in future between the median oblique vein (*Om*) and the cubital oblique vein (*Oc*). This latter is very clearly marked in *Xantholeon* (Text-fig. 2), also in *Glenoleon, Acanthaclisis*, and other genera; but it cannot be satisfactorily made out in our Australian species of the genus *Myrmeleon*, which are more highly specialised.

The process by which *M₂* and *Cu₂* have attained their present positions may be described as a process of "trachea-capture." The two tracheae run at first more or less parallel. As the wing becomes narrower, they come to lie side by side. The oxygen-supply conveyed by both is now no longer fully needed; so that, in course of time, the weaker (in this case the lower) trachea becomes aborted, being reduced to a remnant impinging upon the strong upper trachea from below. In the resulting imaginal wing-venation, however, where the determining factor is not oxygen-supply, but the wing-stresses brought about during forward flight, the vein formed along the course of the lower trachea
continues the line of the stronger upper trachea beyond the point  
where the partially aborted lower trachea ceases to exist, and  
must, therefore, be regarded as a composite vein, whose double  
origin is now only indicated by the oblique vein placed above it.  
Thus, in the case under consideration, we have two composite  
veins formed, viz., the *cubito-median*, \( \text{Cu}_{1a} + \text{M}_2 \) (whose structure  
I worked out in No.1 of this series of Studies), and the *cubito-anal*,  
\( \text{1A} + \text{Cu}_n \) whose existence  
has not been before suspected. The oblique vein  
indicating the presence of the former is \( \text{Om} \), that indicating the presence of  
the latter is \( \text{Oc} \). The complete, correct, amended  
notation for the forewing  
of *Xantholeon helmsi* Tilliard, is given in Text-fig. 2. In Text-fig.3, I offer  
a phylogenetic series of stages to show the evolution of the *Myrmeleontid*  
type from the original archaic formation of these veins, as still  
preserved for us in the archaic *Hemerobiidae, Drepanepteryx*, and  
*Drepanacra*.

*Phylogenetic series illustrating the evolution of the cubitus in the  
wings of *Hemerobiidae* and *Myrmeleontidae*.—Series *a, b, c*, three stages  
leading to the reduced Hemerobiid type, also to the type found in *hindwings* of *Nymphidae* and *Myrmeleontidae*. With *a*, compare forewing of  
*Drepanepteryx*; with *b*, compare hindwing of *Drepanepteryx*; with *c*, compare wings of *Drepanomina*. The final stage, in which the furrow \( f \) is  
completely eliminated, is not shown in this figure.—Series *a, b, d*, three  
stages leading to the formation of the cubito-anal vein in the *forewing* of  
the *Myrmeleontidae*, by fusion of the veins \( \text{1A} \) and \( \text{Cu}_2 \). In *d*, the basal  
part of \( \text{Cu}_2 \) is indicated by the cubital oblique vein \( \text{Oc} \).

Lettering as on p.118, and, in addition, \( k \), the point destined to become  
\( \text{cuf}' \), and \( s \), the sector of \( \text{Cu}_1 \) destined to become \( \text{Cu}_{1b} \).
In Text-fig. 2, c, I have figured the base of the hindwing of Xantholeon helmsi Tillyard, in order to contrast the simplified condition of this wing with the complicated condition of the forewing discussed above. Since the Myrmeleontidae are admittedly derived from Nymphid-like ancestors; and since, in the Nymphidae themselves, both the media and the cubitus of the hindwing are already simple, unbranched veins, it must follow that this condition is to be found in their derivatives, the Myrmeleontidae. It should, however, be noted that there are signs of specialisation even in the hindwing, in that the vein 1A approaches basally very close to Cu, very nearly fusing with it; while Sc and R are completely fused together throughout the basal portion of the wing.

We have now to consider whether our new discoveries on the structure of the cubitus require us to make any revision in the present classification of the Myrmeleontidae. Esben-Petersen, in Part iii. of his "Australian Neuroptera,"* has named the area between Cu₁₂ + M₂, Cu₁₃, and the hindmargin of the wing, the intercubital area, and has pointed out that a Banksian Line is sometimes developed in this space; such a line, he calls the intercubital line. With this I am in agreement. Now the development of an intercubital line is evidence of high specialisation in this area. Therefore, those genera in which it occurs, if they have hitherto been regarded as primitive, must have their position reconsidered. In the tribe Creagrini, this intercubital line is beautifully developed, and is correlated with a condition of parallelism between Cu₁₂ + M₂ and Cu₁₃. It was natural, so long as this latter vein was taken to be Cu₂, that this condition of parallelism should be considered primitive. But the archaic condition existing for Cu₁₃ is not one of parallelism to Cu₁₂ + M₂, but rather, as may be seen in Xantholeon, one of strong divergence from it, Cu₁₃ running obliquely to the margin, and parallel to the numerous branches descending from Cu₁₂ + M₂. Xantholeon, Gymnocnemia, Periclystus, and other genera show this

* These Proceedings, 1917, xlii., Pt. I, pp.203-219, Pl. x.-xv. (Pl. x., fig. 1, Protoplectron striatellum Esb.-Pet.).
primitive condition well. From this primitive state, two lines of development may follow:—

(1) Cu₁ᵇ may become fixed in its divergent position, and the intercubital line may be developed in the usual manner between the descending branches of Cu₁ᵃ + M₂. Various stages in this process may be studied within the genus Glenoleon, while the complete formation may be seen in Acanthaclisis and Myrmeeleon.

(2) Cu₁ᵇ may become straightened out parallel to Cu₁ᵃ + M₂, the intercubital line becoming developed between them, and parallel to both. The beginning of this line of evolution is evident in the forewing of Protoplectron striatellum Esb.-Pet., which is, therefore, fairly primitive. In P. venustum Gerst., the formation is practically completed; while in Creagris plumbeus Ol., (Palaearctic) the development of the three parallel veins, with all connecting structures reduced to simple series of cross-veins, reaches the highest possible stage of evolution along this line.

It would appear, therefore, that my estimate of the tribe Creagrinii, as the most primitive of the Dendroleontinae, is not correct. They form, rather, a separate side-line of development away from the main stem, culminating in a very highly specialised genus, viz., Creagris. It should be noted, in this connection, that the larva of Creagris is the only one amongst the Dendroleontinae that is known to make pit-falls. It will now be of special interest to find out whether the larvae of Protoplectron do likewise.