ON THE WING-VENATION OF INSECTS

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The admirable method discovered by Comstock and Needham,[1] of showing homologies in the wing neuration of various types of insects does not allow us, unfortunately, to discover veins which have disappeared during the course of evolution. It is absolutely necessary to make a study of fossil forms in order to complete the ontogenetic data by means of information derived from the connections and topography of the veins in ancestral types which no longer exist.

No living insect possesses neuration as complete as that of many fossils from the coal measures; the result is that Comstock's[2] scheme of the fundamental primitive neuration is inexact, for it is based on living Perlids. To take this scheme as a basis of comparison leads to confusing entirely different veins under the same heading. That is what has happened notably with the Ephemerids and Odonata, of which the neuration does not seem to me to have been well understood.

We know that ontogentic study shows two tracheæ penetrating the wing; the ramifications of the anterior trachea correspond to the costal, sub-costal, radial, and median nervures; those of the posterior trachea correspond to the cubital and the three anal nervures.

The radial nervure presents two branches: the radial, strictly speaking, and its sector.

In the wings of the Ephemerids, the Odonata, and the Protohemiptera from the coal measures, the median nervure forks, not far from the base of the wing, into two branches which I have termed the anterior median and the posterior median[3]; that is to say the median has exactly the same configuration as the radial, so that the posterior median can be considered as the sector of the anertior median. The comparison of the form of the median

[1]Sur la nervation alaire des Insectes. Bull. Class. des Sci. Acad. Roy. Belgique, 1922 pp. 38-149.

with that of the radial follows, if it is assumed that the radial is a high nervure while its sector is a low nervure; then the anterior median is a high nervure, the posterior a low nervure.

The sector of the median is missing in the Perlids and consequently does not figure in Comstock's scheme. I have shown that this nervure is very short and that it rejoins the cubital, or rather that it is completely lost in all the Orthoptera (*sensu latissimo*, including the Perlids); Tillyard has also shown that the same thing happens to the sector of the median (which he calls M^5) in the Holometabola.[4]

The cubital nervure has a configuration exactly like that of the radial and median; even nearer the base of the wing than does the median, it divides into two branches, an upper anterior, which I have called anterior cubital, and a lower posterior, the the posterior cubital, which is in a way the sector of the cubital.

Thus radial, median, and cubital show an identical form among the primitive insects, consisting of an upper vein followed by a lower sector.

Now we may ask if the same plan does not apply to the other nervures.

The costal is a high nervure, the sub-costal a low nervure, although the sub-costal appears not to be a branch of the costal, but arises directly behind the costal from the anterior tracheal (trunk) of the wing, it seems to me that we must admit that the sub-costal is the sector of the costal.

In the living insects only three anal nervures are found; but an examination of the fossils from the coal measures shows that there are apparently many more, for they are branched. I distinguish a first upper anal, a second lower anal, a third upper anal followed frequently by lower branches. I believe that we find but two anal nervures, the so-called second anal being the sector of the first.

The wing thus contains six (principal) nervures, three forming the anterior group: the costal, the radial, the median; and three belonging to the posterior group: the cubital, a first anal (1A) which we may call the *penultimate*, and a second anal

(3A) which we may call the *ultimate*; each of these six nervures is high and has a low sector.

Consequently we return, in the oldest insects known, to that regular alternation of high nervures and low nervures included in Adolph's old hypothesis. We can even use the nomenclature of J. Redtenbacher, accepted by C. Brongniart, numbering the nervures from I to XII, the odd numbers designating the primary nervures and the even numbers their sectors.

To adapt these ideas to the nomenclature of Comstock and Needhan, which is today universally accepted, I propose to designate all the sectors by the names of their respective nervures, adding to these names the prefix *sub*.

Then we shall have in the first group: the costal, high (C or I), with the sub-costal, low (Sc or II): the radial, high (R or III) with the sub-radial, low (Sr or IV): the median, high (M or V), with the sub-median, low (Sm or VI) and, in the second group: the cubital, high (Cu or VII), with the sub-cubital, low (Scu or VIII): the penultimate, high (P or IX), with the sub-penultimate, low (Sp or X): the ultimate, high (U or XI), with the sub-ultimate, low (Su or XII).

The sub-radial, the median, the sub-median, the cubital and the sub-cubital are each forked twice in the primitive insects, giving two limbs and four branches; we have then, adapting the the data to the accepted nomenclature: Sr^1, Sr^2, Sr^3, Sr^4,; M^1, M^2, M^3, M^4, Sm^1, Sm^2, Sm^3, Sm^4; Cu^1, Cu^2, Cu^3, Cu^4; Scu^1, Scu^2, Scu^3, Scu^4.

The general evolution of insect wings is characterized by a lengthening which is concurrent with a diminution of the breadth; this phenomenon has been accompanied by the disappearance of certain longitudinal nervures; but these are not the same nervures which have disappeared if we consider the two great groups of Pterygota; a misunderstanding of this fact has caused a regrettable confusion.

With all the insects whose embryogeny has caused them to be called Ectoblastic[5]—that is to say the Paurometabola (*sensu latissimo*, the Orthoptera) and the Holometabola,—we have made

mention of them above,—the sub-median as is reduced to a very short nervure rejoining the cubital, or perhaps as is more frequently the case, it aborts completely. What is called the median in the Pterygota (M^1, M^2, M^3 M^4) is then really our own median, that is to say the upper anterior branch of the third nervure of the first group, and there is no change in the terminology.

As for the Endoblastic Pterygota (Subulicornia and Rhynchota) more primitive than the Ecoblastic forms, it is entirely otherwise. Here the neuration is complete, or rather if the longitudinal nervures disappear it is never the sub-median alone, but very often the anterior median and also the anterior cubital, the narrowing of the wing ordinarily involving the spaces adjacent to the sub-median. This I shall have to show by palæontology, for the ontogeny of living forms not only has been insufficient to show this peculiarity, but has at the same time led zoologists to form totally erroneous homologies.

It is in the Ephemeroptera of the group Spilapteridæ from the coal measures that we meet with the most complete neuration; this suits our scheme completely (e. g. Lamproptilia Ch. Brongn.) in certain genera, however, the anterior median and anterior cubital may be simple; that is, not branched.

Everyone agrees in considering the Stephanian genus *Triplosoba* Handl. (Blanchardia Ch. Brongn.), type of the Protephemeroidea, as the precursor of the real Ephemeroidea, which are found already in the Permian; the neuration is the same as that of the Spilapteridæ, in which the anterior median and cubital are represented by a simple nervure (*e. g.*, Apopappus Handl.); but there are adventitious sectors in the sub-radial, sub-median, and sub-cubital spaces; the sub-median is simply forked, and between its branches is an adventitious sector.[7]

Now if we compare the wing of the Ephemeroids of the Permian, Secondary, Tertiary and the present day to that of Triplosoba, the configuration and connections show at once that the lower nervures considered by Comstock as M^1 and M^2 with the adventitious sectors between, correspond to Sr^1 and Sr^4 of Triplosoba, that is to say, the sector of the radial has been wrongly considered a branch of the median, because of the fact

that the latter is reunited at the base, which, from a morphological standpoint, is of only relative importance; it is seen that Comstock's M^3 and M^4, with the adventitious sector between, are Sm^1 and Sm^4; that Cu^1 and Cu^2, low nervures, with the adventitious sector between, are Scu^1 and Scu^4; that 1A, high, is P; 2A, low, is Sp; 3A, high, is U.

The high nervures M and Cu, which are present and simple in Triplosoba, are missing between Sr^4 and Sm^1, in some cases, between Sm^4 and Scu^1 in others; we may consider that they have disappeared, in consequence of the narrowing of the wing, a change which becomes very marked with the Protereismidæ of the Permian.[8]

It is very interesting to show the Sm and its branches are high in the *Ephemeroidea*, while these nervures are low in *Triplosoba*, which brings back the regular alternation of high and low nervures broken up by the disappearance of the adjacent high nervures *M* and *Cu*.

The wings of the Ephemeroidea differ from those of the Protephemeroidea by the reunion of the median with the sector of the radial near the base of the wing, by the disappearance of the anterior high median and cubital, the sub-median and sub-cubital alone remaining, the sub-median having become a high nervure.

Following the conclusion of a work by Miss Morgan[9] Comstock agreed that in the Ephemeroidea the radial sector is represented by a small trachea arising from the radial, not far from the extremity of the wing; he considered as belonging to the sector of the radial the two final added sectors situated in the space which I have called sub-radial, and in which it makes a median space. These authors tried to discover in the wing of the Ephemeroidea the sector of the radial which they did not see, taking it for a branch of the median, and they sought the solution in a comparison with the wing of the Odonata.

None of Miss Morgan's drawings seem to me convincing; the numerous preparations of young larvæ of Ephemeroidea of different genera *Baetis, Clœon, Leptophlebia, Cœnis*) made at the Overmeire biological station by Mr. Paul Brien, student-assis-

tant, have shown us nothing which recalls anything of the singular arrangement existing among the Odonata of the group Anisoptera. We have not seen the small sector trachea described by Miss Morgan; supposing that it really does exist, it has only the value of an adventitious trachea, the only value which can also be attributed to the famous trachea which, according to Comstock and Needham, represented the sector of the radial in the Odonata.

Tillyard, to whom we are indebted for so many fine works on living and fossil insects, recently confirmed the opinion that the subnodal sector of de Selys-Longchamps among the Libellulidæ is the sector of the radial crossing the median nervure.[10] I was for a long time persuaded that this nervure, absent in the Zygoptera, as Tillyard has shown [11] is an additional simple nervure serving in the Anisoptera to close up the sub-radial space which was enlarged during the course of evolution; this nervure, which may be called the secant (S), is a physiological realization of what exists in the Neuroptera, where the enlarged sub-radial space is closed by a supplementary branch of the radial sector.

Tillyard's conclusion is that the neuration of the Odonata can be interpreted only by palæontology.

Here is the reply which I believe I can support, using as a basis what we have learned from the evolution of neuration in the Ephemeroidea, and what the evolution of the Odonatoptera shows us.

In the Odonata, the nervures which all present-day entomologists consider as M^1, M^2, Ms and M^3 are with me the four branches of the sector of the radial, Sr^1, Sr^2, $Sr,^3$ Sr^4, the sector of the radial being, as in the Ephemeroidea, reunited at the base of the median; the upper anterior median (*M*) is represented alone by the high nervure at present designated by the symbol M^4; the posterior median (*Sm*) is absent; the anterior cubital (*Cu*) has disappeared, as in the Ephemeroidea; the nervure considered as Cu^1, low nervure, is the sector of the cubical (*Scu*); the nervure considered as Cu^2, upper nervure, is the first anal or penultimate (P), reunited at the base of the sub-cubital,

the nervure 1*A* of current usage, high, is the third anal or ultimate (*U*), partly attached to the penultimate.

The neuration of the wing of the Libellulidæ would not be exactly similar to that of the Ephemeroidea, contrary to what has been considered heretofore, and the comparison which has been made with that of Ectoblastic insects is rather lame.

The evolution of fossil Odonatoptera, which I have been able to study at the Paris Museum, will show us this.

In the Dictyoneuridæ of the coal measures the primitive neuration is complete and typical, but very often the anterior median and anterior cubital are simple (as in the genus *Stenodictya* Ch. Brongn.)

Dictyoptilus Ch. Brongn., of the Stephanien, has a more elongated wing; the median is contiguous to the radial at the base of the wing, which gives a small pre-costal space,—all characters which are accentuated in the Protodonata[1].

These last have the median confused with the radial at the base of the wing, and the radial sector arises from the median, as in the Ephemeroidea.

Let us now consider *Meganeura Monyi* of Ch. Brongniart, the giant Libellulid of Commentry, and compare its neuration, on one hand with that of Dictoptilus, on the other hand with that of the Odonata, the nervures being for the latter designated according to their current names.[2]

In Meganeura, we see, leaving the common trunk which leads to the radial, a nervure which soon divides into a lower anterior and an upper posterior nervure; the first (Brongniart'sV) corresponds evidently to the radial sector in *Dictyoptilus*, and it divides, as in the latter; into two low nervures Brongniart's IV and V) in which we recognize, on one hand, $M^{1\ 2}$ Ms; on the other, M^3, of the Odonata; the second (Brongniart's VII) is the median in *Dictyoptilus*, which is reunited to the radial at the base of the latter's sector; this median is divided into a high nervure, the anterior median, in which we recognize M^4 of the

[1]See the fine photographic reproductions of the wing of *Dictyoptilus* (*Cockerelliella*) *sepultus* F. Meun, published by Boule in the Annales de Paleontologie, vo. 7, pl. 7, figs. 4, 4a.

[2]The figure of the wings of *Meganeura monyi* in the work of Brongniart (Pl. 42) is correct; in Handlirsch the fore wing is in part inaccurate.

Odanta, and a low nervure, the posterior median; this last the Odonata, and a low nervure, the posterior median; this last is missing in the Odonata, which have retained only the upper anterior median.

From the base of the wing of *Meganeura*, a little behind the radio-median trunk arises a long, winding, simple nerve (Brongniart's VIII) which is very low; comparison with Dictyoptilus shows that it must be the posterior cubital (Scu), as the anterior upper cubital which approaches very near to the posterior median in *Dictyoptilus* is evidently absent. It is certain that this nervure Scu is represented in the Odonata by the low nervure at present known as Cu^1.

Still a third nervure leaves the base of the wing of Meganeura; it is parallel to the posterior cubital and is high (Brongniart's IX); almost on the level at which the radial detaches itself from its sector and from the median, this high nervure gives rise to a low nervure (Brongniart's X); we now have the first and second anal, the penultimate nervure with its sector, and this nervure corresponds to Cu^2 of the Odonata.

We know that in the Odonata a trachea gives rise to Cu^1 and Cu^2, these nervures proceeding from a common trunk, and another trachea furnishes the nervure designated as 1A; this last attaches itself very near the base of the wing to the common trunk of Cu^1 and Cu^2, and then becomes independent.

We have the same thing with Meganeura and even probably with Dictyoptilus; no attention has been paid to it, because Ch. Brongniart has neither seen nor figured anything, except in Meganeura; between the base of the wing and the level of the division of the penultimate into P and Sp, there exists an oblique nervure which attaches the cubital again to the last nervure arising from the base of the wing. [1]It is evidently a case of an anastomosis between the cubital and the penultimate, the latter proceeding thus from the cubital, as in the Odonata. So the last nervure which leaves the base of the wing in *Meganeura* is

[1]This oblique nervure is immediately recognizable in the photographic reproduction of a wing-fragment of Meganeura, given by Bolton (Quart. Journ. Geol. Soc., vol. 70 (1914), pl. 18, fig. 1) and in that of another Meganeura published by Boule (Ann. de Paleont, vol. 4 (1909) pl. 17, fig. 2); E. H. Sellards has figured it in *Typus permianus* (American Journ. Sci., vol. 23 (1907), p. 250, fig. 1, p. 252, fig. 2.

only the ultimate; it corresponds to 1A in the Odonata, and, just as with the latter, it is attached along a certain length to the nervure which precedes it, supporting the secondary nervures which are opposite in direction to those which are supported by the sector of the penultimate. The Protodonata also seem to have three anal nervures, *P*, and *Sp* and *U*, *U* rejoining the common trunk of *P* and *Sp* after this has left *Scu*.

In the Odonata, on account of the attenuation of the base of the wing, the attachment of the sub-cubital and penultimate extends farther than in the Protodonata, the sub-penultimate is missing, and the ultimate is attached in part to the portion common to *Scu* and *P*.

The essential differentiation between the Protodonata and Dictyoptilus lies in the reunion of the median to the base of the radial and the disappearance of the anterior cubital; the Odonata are derived from the Protodonata by the suppression of the posterior median and of the sector of the penultimate nervure.

It remains for us only to inspect the neuration of the Rhynchota. Is what we call the median in Endoblastic insects the nervure *Sm* of the Subulicornia or rather the nervure M of the Ectoblastic insects? The study of existing forms does not permit us to decide. Let us then have recourse to palæontology.

The numerous Protohemiptera of the coal measures[12] offer a complete wing-neuration; but in all the anterior median is simple, and the anterior cubital is ordinarily so.

The real Hemiptera, Rhynchota which undoubtedly descend from the Protohemiptera and of which a representative is known in the Stephanian, have a forked median and cubital, and the two branches of these are ramified. It is sufficient to consider the neuration of the permian genera Scytinoptera and Prosbole, in Handlirsch's Atlas to be presuaded that with neither the Homoptera nor the Heteroptera is there an anterior median or an anterior cubital, that the position of these nervures is occupied by a great empty space and that the two forked nervures are the sector of the median and the sector of the cubital.

The evolution of neuration in the Hemiptera thus takes

place in the same way as with the Ephemeroptera, a new proof that the Endoblastic insects may be placed opposite to the Ectoblastic in classification.

Conclusion.

The scheme of primordial wing neuration worked out by Comstock is useful only for Ectoblastic insects, which have lost the posterior branch of the median nervure, and that since their appearance in the coal measures.

The Endoblastic forms, Subulicornia and Rhynchota have, for the most part, in the coal measures, a complete neuration conforming to a scheme in which six low nervures alternate with six high nervures; those between in which the wings do not agree with this type, notably all the forms which have persisted beyond the Permian, have lost other longitudinal nervures than the Ectoblasts.

The Ephemeroptera, the Protodonata, the Odonata, and the Hemiptera do not possess the anterior branch of the cubital nervure; the Ephemeroptera and Hemiptera lack also the anterior branch of the median nervure; the Protodonata, as well as the Odonata, have retained this, but the Odonata have lost the posterior branch of the median nervure.

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