THE INTERPRETATION OF THE WING VENATION
AND TRACHEATION OF THE ODONATA
AND AGNATHA.¹

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INTRODUCTION

In 1922 Dr. A. V. Martynov read a paper before the
Entomological Society of Russia on the interpretation of
the veins and tracheae in the wings of the Odonata and
Agnatha (Plectoptera). His manuscript was turned over
for publication in 1923 and after some delay was finally
published in Russian the following year (Rev. Russe Ent.,
18(4):145-174). In connection with my investigations on
fossil insects, I found it necessary to consult his paper,
and from the very short French summary at the end of
the article, I felt sure that the text contained important
data and discussions which should not be overlooked. I
therefore employed Miss Olga Jahr, of the Slavic Depart-
ment of the Harvard Library, to assist me with the trans-
lation of the Russian. Naturally enough, Miss Jahr was
unfamiliar with the biological terms, but by working to-
gether we obtained a complete English translation without
much difficulty. As the translation progressed it became
more and more evident that the text was fully as important

¹This paper is an enlargement of the report which was read at
the Russian Entomological Society, November, 1922; the manuscript
was handed to the press in May, 1923.

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as I anticipated, and when the task was finished, I decided to publish the entire translation of this paper in order that it might be available to other investigators of insect phylogeny. Although there are several points on which I cannot agree with Dr. Martynov, I nevertheless consider this paper one of the outstanding contributions to insect phylogeny published during the past decade.

Dr. Martynov kindly assisted me in locating several misprints which occurred in the original text, and which had naturally caused me much confusion. The twelve figures accompanying the original article are essential for a complete understanding of the problems under discussion. Unfortunately, these figures were very poorly printed, and could not be copied for reproduction here without considerable retouching. Since there is always a possibility of distorting a figure during this process I decided that it would be better not to reprint the figures at all, but to refer the reader to the original ones. While this procedure, involving the use of two publications, may be somewhat inconvenient, I believe it introduces the lesser of two "evils."

—F. M. CARPENTER.

Comstock and Needham published (4) their first data on the interpretation of venation of the Odonata and Agnatha in a series of articles on the wings of insects, which appeared in 1898 and 1899; and in 1903 Needham developed (10) these ideas with more details into a large work on the venation of Odonata. The interpretation of Odonate venation which was proposed in both works mentioned above was later accepted by the majority of Odonatologists and by Handlirsch (6). According to this interpretation the nervuration of the Odonata proved to be so peculiar that it could hardly be compared even with that of the Agnatha—the very closest group.

The most characteristic features of this venational system are the following: 1, the crossing of the radial sector by the bases of $M_1$ and $M_2$, and its extension into the region between $M_2$ and $M_3$. 2, the large size of the media, with 4 branches; $M_4$ always leading from the base of $M$. 
3, the curve of the cubitus (chiefly in the Anisoptera) and beyond this curve, the formation of the two branches, Cu, and Cu₂; formation of a triangle (or quadrilateral. 4, small size of the anal vein and its fusion with the cubitus.

It is necessary to add that according to the authors’ understanding the continuation of RS to M₁₂ is clearly a secondary vein ("bridge") and appears to be the basal part of the analogous vein indicated by Tillyard (14).

The venation of the Agnatha, as usually interpreted (Eaton, Comstock 1899, Handlirsch, Ulmer and others), is entirely different from that of the Odonata, and much more similar to that found in the more primitive Palaeo-dictyoptera (Dictyoneuridæ). The media is simple and forks only in the distal part; RS is large and forms 4-5 branches; Cu is divided at the base, and the down curve is formed only by the lower branch; the anal veins are well developed. These differences in the interpretation of the wings of the Odonata and Agnatha are so great that the dragon-flies would on this basis be moved far off from the may-flies; but this contradicts the sum of all data in morphology and the development of these insects. If venation means anything in the explanation of phylogenetic relations of the different groups—as is unquestionably so, and the venation of the dragon-flies has been studied particularly carefully from this point of view—then either the evidence of morphology and history of development, which indicate a close relationship of the Odonata and Agnatha, are wrong; or the interpretation of the wing venation of Odonata or perhaps the Agnatha is incorrect. As the close relation between the Odonata and Agnatha is not disputed, the author began to doubt the accuracy of the usual interpretation of venation of the may-flies and partly of the dragon-flies.

It is well-known that Comstock and Needham based their interpretation of the wing venation in different groups on the study of the tracheation of the wings of nymphs and pupæ. This tracheation, it is supposed, reflects the more primitive condition of venation. The trachea RS of the Odonata (Anisoptera) turns off from R and, after crossing the bases of tracheæ M₁ and M₂, enters the region between
M₂ and M₃; treacheæ which go into these latter veins and into M₄ of the authors, join at the base into one common trunk, which enters the wing independently. Hence the conclusion that this trunk is M, that RS crosses M₁ and M₂, that the bridge is a secondary formation, that the cubitus is two-branched, etc. Among the may-flies Comstock discovered at first a type of tracheation very different from that of the dragon-flies, and nearer to the normal. From this tracheation Comstock was led to an interpretation essentially similar (if not in names) to the one of Eaton (5) and other authors. Ann Morgan (8) undertook a careful investigation of the tracheation of different species of may-fly nymphs and discovered that the tracheal stem which sends small tracheæ into the branches of Comstock's RS usually arises independently from the common tracheal wing stem. Consequently, she concluded that the system of veins which include these tracheæ do not represent RS, but M, as in the Odonata. Usually in the may-flies the trachea RS does not arise from the trachea R, as it does in dragon-flies; but in one species of Heptagenia, and even then only in part of this specimen, Morgan succeeded in finding a weak trachea which led off from R, crossed M and entered into the region between M₁ and M₂. Following the ontogenetic method of Comstock, Morgan concluded that the may-flies also originally had the radial sector cross the media.

Comstock, in his later work on the wings of insects (3), which represents an enlarged and somewhat changed edition of the joint work of Comstock and Needham (4), agreed with the results of Morgan and accepted, therefore, her interpretation of the wing venation of may-flies. By this interpretation the venation of the may-flies was brought (to a certain degree) up to the scheme of the venation of the dragon-flies; but by the same interpretation the Ephemeroptera venation appeared to be extremely remote from that of the Paleodictyoptera and even the Carboniferous Triplosobidae Handl. Although the latter are placed in

²Only to a certain degree, because Rs of the may-flies in Morgan's paper is not this vein in the dragon-flies. In the latter Rs (of author's) corresponds to our Rs₁ and Rs (Morgan and Comstock) of the may-flies corresponds to our Rs₃.
a special group by Handlirsch, Protephemeroidea, which combines the characteristic venational features of the more primitive *Dictyoneuridae* and the specialized features of may-flies, nevertheless they still are Ephemerids, which preserved only the anterior branch of M of the *Dictyoneuridae* (MA). As to the dragon-flies, Needham’s interpretation aroused doubts only in its application to the Zygoptera. The trachea which supplies RS in the latter arises from M₂, not from R, and in general no tracheae which lead from R enter into the region of M. But Comstock and Needham think that here also, the vein RS enters into the region between M₂ and M₃, and that trachea RS used to arise from R and cross the media, but later “detached” itself from R and “attached” itself to M₂. Since it is difficult to support the last supposition by definite proofs—there are none—Tillyard (15) and Rice (12) naturally expressed doubts about the Zygoptera having RS. Munz, however, pointed out (9) that the conformity of the vain veins of Zygoptera and Anisoptera is so evident that it is impossible to interpret the venation of Zygoptera different from that of the Anisoptera, and accepted the old scheme of Needham.

As I approached the study of the venation of dragon-flies and may-flies I thought that if the dragon-flies and Ephemerids were Palæoptera, i.e., insects which never fold their wings on the back (roof-like) at rest, then not only the may-flies but also the dragon-flies should preserve the features of venation of the related Palæodictyoptera. If the venation of dragon-flies, according to the interpretation of Comstock and Needham, proves to be so unusual that it puts them in an entirely isolated group among the insects, the cause of such a situation evidently lies in the wrong interpretation of the venation by these authors and the uncertainties of the ontogenetic method. It is necessary to note that at one time Redtenbach (11) offered an entirely different interpretation of the venation of dragon-flies; attaching great importance to the alternation of con-

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38 Citing after Munz (9).

4 Concerning the division of the Pterygota into Paleoptera and Neoptera, see my paper (7).
cavities and convexities of the wing, the author compared their dispositions in dragon-flies and may-flies, and came to the conclusion that they are very similar in venation as well as in the alternation of concavities and convexities. Unfortunately this author, following the erroneous conception of Adolf (1) concerning the different origins of “convex” and “concave” veins in the first stage of the “fan” type of wing and the disappearance in other insects of a series of “concave” veins, came to an incorrect homologization of the veins of the two groups mentioned with those of other insects. Thus the cubitus of Ephemerids (and dragon-flies) he indicates by the number viii, which in other insects corresponds to A1; the median by number vii, which corresponds to the cubitus, etc. Denouncing the earlier views of Adolf, Comstock and Needham also did not attach any importance to the similarity in the wing venation between the may-flies and dragon-flies, which was observed by Redtenbach.

It always seemed to me very risky to depend upon Comstock’s and Needham’s ontogenetic method for the explanation of the homology and evolution of venation. When we study the tracheation of nymphs and pupae we study at the same time the ontogeny of tracheation, but not venation at all, because veins are vessel-like forms in which the blood circulates and into which nerves and usually tracheae often enter; but there can exist veins without tracheae. On the other hand, the thinner tracheae which we observe in the nymphs and young imagines of dragon-flies and nymphs of may-flies go through the wing and outside of veins in great numbers and often do not connect the neighboring veins, but the ones lying far apart. As to the formation of veins, although it was previously supposed that they were formed originally by the tracheae, more recent investigations have shown, especially in rather primitive groups [see, for example, the work of Marshall (17) on the development of the wings of the Trichoptera], that in the wing anlage the venation is formed before the tracheae pierce through. Comstock and Needham supposed that the tracheation in the wing of a pupa and nymph reflects the primitive state of venation. Therefore one would suppose that in the forms with a venation which resembles
especially closely the scheme of the original venation, we should expect a particularly complete parallelism of the tracheation with the venation. But this is not so. In Hydropsyche, which is a small caddis-fly with extremely primitive venation, Comstock and Needham found a complete unconformity of the tracheation with the venation, which they interpret without regard for the direction of the trachea. These authors are obliged to do the same with the Hymenoptera and Diptera. Why should we rely so blindly upon the tracheation in case of dragon-flies and Ephemerids and ignore the data of paleontology, which proves the close relation of venation in contemporary representatives of dragon-flies and may-flies with that of the Paleodictyoptera (in the case of the Ephemerids, through the Carboniferous Triplosoba Handl.)? Such a "conception" is all the more unacceptable because the theory of Comstock and Needham encounters serious contradictions within the groups themselves. The crossing of the media which arises from R by means of the trachea RS takes place only in the Anisoptera; this does not appear in the Zygoptera, and the trachea of the corresponding vein arises from the branch M. We have no proofs that the latter condition developed from the former. As to the Anisozygoptera, in view of their very close relationship to the Agrionidae (through the Lestinae), one can suppose that in them the trachea RS of the authors arises from the media of the authors. A very diverse and changeable tracheation of nymphs of may-flies gives us still less right to conclude that they have such a crossing, that their complicated vein below R is M, etc.

My investigation of the relation of the venation to the tracheation has led me to the conclusion that the formation of venation occurred under the influence of causes of mechanical character; the tracheation, adapting itself to the newly formed distribution of veins, often changed in a most original way; therefore, one can judge the venation by such an "indirect" representation of it only with utmost care.

In view of these facts I decided that in investigating the venation of dragon-flies and may-flies, as well as of other groups, to turn first to the comparative study of the vena-
tion itself, at the same time constantly keeping in mind as much as possible the function of the venation, and changes which should appear in the phylogeny of the wing by the work of the separate parts of the wing and the work of its veins. Only after such investigation is it possible to approach the study of the history of tracheation, which depends upon the venation and reflects its history. This I will discuss at the end of this paper.

Let us first turn to the Palæodictyoptera. The "family" Dictyoneuridæ has the most primitive venation (figs. 1 and 2); the wings here are homonomous, hardly broadened at the base; sometimes their ends are somewhat pulled out and as if curved backwards (Stenodictya, Microdictya, Stilbocrocis, Polioptenus, et al). RS in the more primitive forms (Stenodictya, Microdictya) arises from R approximately at the middle of the wing, or a little nearer to the base; but in the majority of other forms we encounter the process of its receding towards the base. Usually RS sends 3 or 4 branches posteriorly, not counting its continuation; in some cases the second branch (counting from the base) does not reach the trunk RS, but adjoins to the first and sometimes (Microdictya vaillanti, Stilbocrocis, Eumecoptera) forks dichotomously. The media is divided into two branches, which we shall call M. anterior (MA) and M. posterior (MP)\(^5\); MA in this family, as well as in the majority of other Palæodictyoptera remains simple; MP branches in the Dictyoneuridæ, often forming three branches (Stilbocrocis, Eumecoptera, Dictyoneurula, Acanthodictyon, partly Polioptenus), in which it greatly reminds us of M in the Ephemerids. Normally the cubitus also divides not far from the base into two branches of which the first (anterior), CuA, usually remains simple as in Polioptenus and Eumecoptera (figs. 1 and 2); the posterior branch, CuP*, usually gives rise to smaller branches.

In the very primitive forms the anal veins form a comparatively homogeneous series of 3-4 veins, which gradu-

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\(^5\) The development and configuration of the media have just the same characteristics as R. MA corresponds to the radius proper (R); MP, to the radial sector. The same was originally true of the cubitus (Cu).

* Misprinted MP in original.
ally grow smaller nearer to the base; but the more specialized A1 is better developed, and others lose their indepen-
dence, uniting either with A2 or even together with A1.

There is no need to discuss the other families, because
their wings were already specialized in different directions
from those in which the dragon-flies and Ephemerids are
specialized.

All recent Agnatha differ sharply from the Palæodicty-
optera, in that their fore wings are greatly enlarged at
the expense of the hind pair (fig. 4), which have become
completely reduced in many species (in sub-group Bætoidea
Ulm.). If the hind wings are present, the fore wings
are wide and approximate a triangle; then, where the hind
wings tend to disappear, the fore wings take the shape in
the first group (Ephemeroidea and Heptagenioidae), which
corresponds more to the shape of the fore and hind wings
taken together.

If the hind wings of contemporary Ephemerids differ
greatly from the fore wings, this was not the case in the
past. In the Ephemerids of the Permian the hind wings
differed very little or not at all from the fore pair, and
their form resembled very much that of the wings of Dic-
tyoneuridæ (13). Likewise, the wings of the remarkable
Carboniferous Ephemerid Triplosoba Brogn. were homo-
nomous (fig. 3). Handlirsch placed (6) this form into a
special order, Protephemeroidea, because it preserved in its
venation the features of the Palæodictyoptera, particularly
of the Dictyoneuridæ. Just as in Eumecoptera (fig. 2)
and in many other Dictyoneuridæ, RS arises nearer to the
base and sends posteriorly the usual four branches, of
which (and this is very important) the second branch, i. e.
RS4, originates near RS5, and RS3 and RS2, together with
RS1, form the distal group. Evidently RS2, already form-
ing the “inserted sector,” did not reach RS1. M, as in
the Dictyoneuridæ, is divided near the base into the same
two branches, MA and MP; MA also, as in the Dicty-
oneuridæ, remains simple, while MP is divided distally into
three branches, the middle one and the two supplementary
ones beside it being already changed into “inserted sectors”
(Schaltsectoren). The close similarity of this MP with
M in the real Ephemerids leads us to believe that M of
the may-flies is really MP, and their MA is reduced and has completely vanished. Cu is divided into two simple branches, in which one can also see CuA and CuP of the Palæodictyoptera. Then come the anal veins; the long A₁ with its branches, and another long one, A₂ or A₃, with its branches. The character of the cross-veins is the same as in Ephemerids. As already mentioned the fore and hind wings in the may-flies of the Permian were alike, their shapes quite resembling those of the Dictyoneurid wings; but in all that is known to us, MA was already missing. The branching of RS is also very much like that of Triplosoba and of the contemporary Ephemerids, while here also (Protechta Sell., Protereisma Sell.) RS₄ arises near RS₅, and the rest of the branches form the distal group. The branches RS₁ and RS₂ represent “inserted sectors” as in the recent Ephemerids.

According to the interpretation of Sellards and Handlirsch, Cu is divided into two branches at the very base; the anterior of these also divides into two side branchlets and a middle “inserted” one (in Protechma); and the posterior branch gives rise to two small branches directed posteriorly. The anal region is badly preserved. On account of this poorly preserved anal region it is difficult to say how to regard the two branches of the cubitus, whether they correspond to CuA and CuP of the Palæodictyoptera or whether there is another interpretation possible. Incidentally, the anterior branch with its branchlets is very much like the cubitus of Siphluridæ, Ecdyuridæ or Leptophlebiidæ.

The fore wings of the recent may-flies, because of the division of labor between the wings (all work of production of strokes and stroking the air being transferred to the fore wings), increased their dimensions and took the shape of elongate triangles, as in many Papilionidæ; as to the hind wings, where they are developed best of all—in Ephemeroidea and Heptagenioidea—they are of an oval or round shape as in many Rhopalocera, and in other may-flies—in Bætidæ, Ephemereellidæ, and Cænidæ—they are subject to greatest reduction. The fore wings, substituting in these groups for the disappearing hind ones, grow wider in the cubital and anal region and take a shape which
corresponds to the form of the fore plus hind wings in other groups, or to one wing of the homonomous group (Dictyoneuridae, Carboniferous and Permian Ephemerids). Therefore, I think that the primitiveness of Bætoidea wings is only an apparent one and that in the past their fore wings were also probably of triangular shape. The differences in dimensions and in the shape of both pairs, in their turn also, were formed for a second time, replacing the original homonomous condition. The venation inherited from the ancestors was not effected by the change in the shape of the wings, and it remained very much like that of such may-flies of the Permian as Protereumisma, Protechma, and also as Triplosoba. The homologizing of veins in these last forms with those in the Dictyoneuridae is therefore not difficult and is correctly interpreted by Handlirsch. RS in Triplosoba also turned off (from R) at the very base, but here the place of origin (how, is another question) is still nearer to the base. But more often Rs is derived (secondarily) from the basal part of M.* The branching of RS is entirely similar to that of the Palæozoic may-flies and to that of the majority of Dictyoneuridae, i. e., RS forms two groups: a basal branch, and another one almost always without a basal connection, the “inserted sector,” Rs₂; and the distal one, including RS₁, RS₂, and RS₃, the sector RS₂ having already lost its true origin (“Schaltsector”). In the hind wings, because of their reduction, the branches of RS are very seldom preserved, as in Palingenia; usually only RS₃ and RS₄, and naturally RS₁, are preserved, but RS₃ and RS₂ retreat towards the edge and are reduced. M corresponds to MP in the Triplosobidae and Dictyoneuridae, and forms the usual three branches. The branches of M in the hind wings are reduced also, and usually are simple (fig. 10). At the base of the fore wings, M approaches R almost to contact, and weakening, disappears; in the hind wings M often fuses at the base with R. Into this narrow path RS is directed and usually diverges from M, but often ends here as an “inserted sector,” i. e., it weakens and disappears, being joined basally with R and M by means of the usual cross-veins. In the hind wings,

* Misprinted M₁ in original.
RS arises either from R or oftener from M. As well known, RS and M are tracheated in the may-flies in the majority of cases from one main trunk, which turns away from the side trachea (in the body), independently from R. This condition and perhaps also the fact that RS oftener "turns away" from M, gave Anne Morgan the motive to assert that the complicated vein which Comstock originally (4) indicated as RS, is actually M. We shall return below to the explanation of this moving off of RS from M, but now let us turn to the following veins.

Cu arises near M and soon divides into two main branches; Cu₁ and Cu₂, with an inserted middle branch which joins at the base either to Cu₁ or Cu₂ ("inserted sector"). In all Ephemeroidea (Palingeniidae, Ephemeridae, Polymitarcidae, Potamantidae), Cu₂ forms a downward curve similar to the curve of the cubitus in dragon-flies. By means of its projecting angle, this curve approaches and often completely fuses with A₁. The cross-veins disappear between the very origins of Cu₁ and Cu₂; on account of this, in my mind, they correspond morphologically as well as physiologically to the triangle of the dragon-flies (Anisoptera). In Heptagenoidea and Bætoidea this curve is absent (except in Bætisca, Oniscigaster), or it is expressed very faintly. The basal bifurcation and the general configuration of the origin of the cubitus in Ephemeroidea are certainly secondary if compared to, e. g., their condition in Dictyoneuridae. The condition in Siphloridae (and perhaps in the Ephemers of the Permian) is therefore less changed.⁶ The peculiar condition in Ephemeroidea originated in the receding of the furcation point towards the base (this is a very common condition among the Palæodictyoptera, and in Ephemers it unquestionably took place in RS), and by forming the curve in Cu₂. This connection with A₁, just as that in the dragon-flies, has unquestionably mechanical advantages, although the method itself and the original causes of the curve in Cu₂ are not clear to us. It is difficult to say yet if one can see in our Cu₁ and

⁶However, it is possible that in some Siphloridae the curve of Cu₂ was lost secondarily; the condition in Oniscigaster is especially suggestive of this.
Cu₂ of the Ephemerids CuA and CuP. The similarity with the dragon-flies seems to confirm it, but their palaeontological data do not assert this with certainty, and I indicate these branches so far by different symbols.

In groups with the curve of Cu₂ present A₁ also has a more or less considerable curvature. Often the descending segment of Cu fuses entirely with the original of A₁, a condition which we encounter in some Palingeniidæ (Anagenesia, Plethogenesia), or otherwise disappears (Campsurus, Polymitarcyæ, et al). Ordinarily A₁ forms distally a series of branches directed posteriorly. It usually also has an upward curvature. A₂ arises either in the middle of A₁ and A₃, or very close to A₁; usually it curves backwards soon after, and becomes short, and only in Bætiscidæ does it run parallel to the straight A₁. A₃ is still shorter, but often has more branches; in Bætisca its first branch is parallel to A₂. From the distal part of these (A₃) lead a few weak anal veins, but more often the latter lose their independence, and come in contact with A₃ in different ways.

In groups which have the tendency to a final reduction of the hind wings, the cubito-anal regions of the fore wings grow, take the place of the disappearing hind wings in function, and correspondingly elongate and distribute the anal branches in accordance with the mechanical needs (Cænidæ, Bætidae, Leptophibidæ). The anal veins preserve the more original bow-shaped form in the hind wings, but quickly weaken towards the base.

Now let us turn to the question of concave and convex veins, and to their relation to the veins in the wings of may-flies. In 1880 Adolf noted the fact that in the wings of may-flies the concave ones, like valleys, alternate with the convex, as longitudinal ridges. In the bottom of valleys and on the peaks of ridges are the adjoining longitudinal veins. Adolf regarded this alternation as very important. According to his understanding the "convex" and the "concave" veins have entirely different origins, significance and destinations. He thought that the original wings differed in the possession of a more regular alternation of the numerous convex and concave veins and that the wings
were similar to a fan. Redtenbach compared fully the distribution of these veins in the may-flies and dragon-flies, and found a complete correspondence. Later it was shown (2) that the indicated representation of Adolf was incorrect and perhaps this was the cause of Comstock's and Needham's paying little attention to the valuable comparisons of Redtenbach. The plaiting and alternative distribution of veins along the bottoms and tops has great mechanical value. The wings of the may-fly have attained a very high specialization. The membrane is extremely thin and delicate, and its veins have already adopted an extraordinary mechanical function and acquired the corresponding structure (ribs, absence of blood, dry structure) and their distribution also corresponds to the mechanical requirements. If this thin membrane were spread over the veins entirely in one plane, then at the stroke of the wings upon the air, being so delicate and unable to stretch, it would break and inevitably tear. The plaiting gives the membrane flexible, elastic qualities. At the sharp resistance of air on the stroke of the wings, the latter can stretch sufficiently because of the plaiting at all necessary points. In the formation of this plaiting the closely lying veins, as in similar cases (Arthoptera), were distributed, some on the bottom, others on top, and their course, even in their details, was affected by the plaiting; the fundamental character of the latter, in its turn, was conditioned by the original distribution of veins. In that way the continual reciprocal action of these two structures took place in the course of evolution. The concave position among the main veins includes Sc, RS, Cu and A2, and then a series of distal branches, which alternate with the convex greater part of the distal sectors, Cuad7, Mad, RS4, the RS3 concave, RS2 convex; among the smaller distal sectors, the larger ones also alternate. In the more primitive Pal-ingeniidae, Ephemeridae, Ecdyridae and the ones near to them, which retain rich, thick venation in their wing, the greater part of the distal sectors, Cuad7, Mad, RS4, the branches between RS2 and RS3 as well as these branches

7Cu additional or M additional; in this way we shall designate the middle branches of Cu and M.
themselves weaken at their origin and appear to be tied to the neighboring veins only through common cross-veins; and already have no real basal part of their own, nor any origin. Such absence of the origin is unquestionably a secondary condition. In Palingenia and in some Ephemera, RS₄ arises normally from the trunk RS, but in others its origin disappears. The same seems to be the case with other sectors. In the specialized Bætoidea this process went still further, and in Bætidæ all the longitudinal veins except the main ones (Sc, R, RS, RS₅, M₁, Cu₁, A₁, A₂, A₃), lost their origins and became “independents,” Woodworth (16) and the distal ones became shorter and shorter and deteriorated into a series of small veins along the edge, like the measurements on a ruler. How can one explain such a change? It can be satisfactorily explained through mechanical and practical means. The longitudinal veins lose their origins where they enter by means of their bases into the space between the branches of the forking vein, which forms a sharp angle, for example, RS or M. Such a vein is of course always “convex” if the dichotomating one is concave, and vice versa. Because the part of support rests always upon the branching vein, the mechanical meaning of the basal part of the intervening vein diminishes and becomes insignificant; consequently the basal part of such a vein weakens, becomes thinner and disappears entirely. The economy of material requires the disappearance of the unnecessary part of the vein. Everyone knows that in the more specialized and (so to speak) “mechanized” wings, as those of the Bætidæ, all superfluous veins disappear, and the remaining ones tend to keep the intervals between themselves equal. If the origins of the “inserted sectors” remained, this would be an injurious accumulation of veins in different places. The disappearance of the base also requires the alternative distribution of veins in different planes. If the vein is “concave,” and the “inserted” vein, e. g., RS₄, is “convex,” then near the union with RS the short and weak part of the base would have a broken-up aspect (from the convex side to the concave). The mechanical meaning of this broken-up part is insignificant, therefore it

* Misprinted R₁, RS₅ in original.
would unquestionably weaken and finally disappear. Such was, according to my understanding, the way in which the "inserted sectors" of the German authors were formed. Now, the origin of RS sometimes from M, more seldom from R, or its "free" origin becomes clear to us. Entering into the oblique angle between the convex R and M, the concave RS unquestionably had to become a "Schaltssector," which we quite often find in the typical species of Hexagenia, in some Siphlurus and others. The approach of the base of RS to one of the neighboring veins, e. g., to M, together with some small changes in the direction of the joining cross-vein (the cross-veins are certainly preserved) easily give the appearance that RS arose from M.

The appearance of the alternation of the convex and concave vein with its result—the change of convex veins into "inserted sectors"—had been acquired by the ancestors of may-flies and dragon-flies very long ago. This appearance was well expressed not only in the may-flies of the Permian, but also in the Carboniferous Triplosobidae, as becomes clear from their possession of a series of "inserted sectors." The dragon-flies of the Mesozoic do not differ in this respect from the recent ones. The Carboniferous "Protoodonata," at least some of them, also acquired this alternation. The plaiting was already indicated in the Paleodictyoptera and Megasecoptera but it was very seldom that the branches actually turned into inserted sectors, and according to the branches we can judge with certainty about this

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8 Woodworth, on the contrary, sees in the "independent" veins of the may-flies primitive structures which illustrate the process of the formation of the longitudinal veins of insects. The "independent" veins are supposed to receive their origins from the marginal vein, as growths of the latter to the inside; these growths are pulled out towards the base and finally fuse with one of the main trunks. The media, according to Woodworth, was formed as an independent vein also, only the anal veins having a different origin, and growing from the base. We have no need to stop to discuss this fantastic theory; it contradicts all data of paleontology and comparative systematics (the condition in Betoidea is unquestionably secondary!), and is impossible from a morphological aspect. (One cannot imagine the growth of veins in the membrane.)

4 I do not exclude the possibility that some (short) intercalary veins of dragon-flies could develop as illustrated by Comstock (1918): as a result of the formation of plaiting.
plaiting. Such was the situation acquired, e. g., in *Camplyoptera eatoni* Brongn., a species referred by Handlirsch to the Megasecoptera. In the drawing by Handlirsch the character of the intercalary sectors is very clear. Furthermore, according to Handlirsch's drawing the change of some longitudinal veins into intercalary sectors had begun in Lycocercus and in Epithethe. In other Palæodictyoptera we do not notice this. In groups rich with longitudinal veins as the Spilapteridæ, Lamproptilidæ, Polycræagridæ, the plaiting was already suggested, but it never came to a formation of inserted sectors. The plaiting, together with the forming of inserted branches, is a very important mechanical improvement, which allowed lightening of the wing a great deal without loss of its firmness and elasticity.

Leaving aside for awhile the question of the origin of the peculiarities of tracheation in may-flies, which we will consider together with the tracheation of dragon-flies, let us turn to the venation of dragon-flies. The peculiarities of dragon-flies enumerated at the very beginning of this article, are, as stated, rather the peculiarities of interpretation, which result from the nature and insufficiency of the method employed ("method of ontogeny"), and not at all from the actual venation. Putting aside these hypothetical considerations, let us compare the wings of dragon-flies with those of may-flies and Palæodictyoptera.

First of all one should note that in form as well as in the general distribution of the main longitudinal veins and in the smaller reduction of the anal area, the Anisozygoptera show a great deal more primitive features than the Zygoptera, whose wings were subject to very great changes; one could say that in the Anisozygoptera everything in general is much closer to the Zygoptera, and as a matter of fact merges into them in their more primitive Liassic representatives (Archithemidæ, Heterophilebiidæ); they still partly resemble the Anisozygoptera in their form, configuration of the anal area, and in general distribution of the main veins.

In this collective Liassic complex the triangle (e. g., in Heterophilebiidæ) begins to take form, but further development was reserved only for such groups in which the triangle succeeded in acquiring its typical aspect,—and these were the groups that formed the Anisozygoptera; others, where
the "attempts" did not lead to the form of a typical triangle, died out. From here by way of another evolutionary path of the Zygoptera, were derived the majority of the known Anisozygoptera, which often cannot be told apart from the Zygoptera.

Unquestionable Zygoptera and Anisoptera are known only as far back as the Jurassic. The form of the wings in the Anisoptera and still more in the primitive Archithemidæ, resembles very much that of the wings of the Dictyoneuridæ, the most primitive of the Palæodictyoptera, also the Spilapteridæ, Triplosobidæ and may-flies of the Permian. If these dragon-flies have remained unchanged in their original form and homonomous nature of wings, we have also the right to expect a general plan of the distribution of veins, because the one and the other are bound together by function. This we actually find takes place. In Diastatomma (Archithemidae) no nodus is to be found and Sc has the same aspect and same relation to R as it has in the majority of Dictyoneuridæ and Spilapteridæ. The next longitudinal vein after R gives rise to 3 or 4 branches; their method of origin and general distribution repeats that in a series of Dictyoneuridæ and Spilapteridæ (e. g., in Stenodictya, Polioptenus, Acanthodictyon, Eumecoptera and others), and still more of Triplosoba and the Agnatha. The resemblance of the Triplosobidæ in the distribution of the branches of RS, especially to the Anisoptera, and to the recent may-flies is so striking and obvious, that we can compare vein by vein without difficulty. In the dragon-flies we usually find in the region of RS two groups, the basal, —formed by the first concave branch, as in may-flies (RS₃ = M₃ of authors) ; and the second convex and also usually "inserted" branch (RS₂ = 1 Morgan) ; and the distal group, formed by the concave RS₃ the weak convex and sometimes almost disappearing inserted RS₂, and lastly the concave continuation of RS (as in may-flies and Triplosoba). After this complicated RS follows the simple vein which is divided from it at the very areculus, and which is indicated by Odonatologists as M₄, but which represents M. It is still impossible to say whether this M corresponds to MA or MP of Triplosoba, and that is why we shall indicate it simply by the letter M. At its base M turns sharply towards R
(as in may-flies) and almost fuses with it, but not entirely: by looking from above (partly), and in a cross-section the partition between the two veins is still distinct. The origin of RS from this turning-point of M, which sometimes has the form of a cross-vein, is not clear to us. RS arises here from the base of M just as in may-flies and one certainly should look upon such a manner of origin as a secondary appearance, even if this tendency was acquired very long ago, for it was already present in the dragon-flies of the Liassic and Jurassic. After this vein follows Cu (CuP) which forms in the Anisoptera and Anisozygoptera, soon after its origin, a more or less sharp curve or projection posteriorly, as in the suborder Ephemeroidea. This curve is still entirely distinct in the Agrionidae, which appear to be the continuation of the Anisozygoptera, and dissappears only in the species of Calopterygidae (by the "straightening" of Cu and A).

Now, if we compare the relation of the longitudinal veins to the convexities and concavities in dragon-flies to that in may-flies, we will ascertain the identity of their distribution, which was well explained by Redtenbacher. This circumstance, certainly, proves once more the correctness of our comparison of RS in dragon-flies (=M of the authors) to RS in may-flies, etc. Cu (Cu+Cu₁ of the authors) is concave, as in the may-flies, and the next vein after it, which consists of the "anal bridge"+Cu₂ of the authors, forms the same kind of projection and is just as "convex" as in Ephemeroidea Ulm. This vein is unquestionably A₁, and Cu₁ of the authors is Cu₂, and to be even more exact, it is CuP. In the majority of the Anisoptera, A₁ comes into contact with Cu after the projection, but such contact, which often changes into fusion, is also frequent in the Ephemeroidea. On the other hand, in the majority of Zygoptera and Anisozygoptera and many other Anisoptera (compare Fig. 6, wing of fossil Heterophlebia dislocata, with Fig. 7, hind wing of Phylloptalia apicalis Seyls), A₁ does not come in contact with Cu and runs independently and almost parallel to Cu. In its general appearance of A₁ (Cu₂ of the authors) of the dragon-flies, especially such as the Gomphidae or Anisozygoptera, corresponds entirely to A₁ of may-flies, analogously forming an arch towards the front and analogously sending a
certain number of weak branches posteriorly. Next follows
in the may-flies the concave A₂, then the convex A₃. But
even if these veins did exist for a long time in the dragon-
flies, they are fused now with A₁ at the base, and in the
majority of cases this region has suffered great reduction.
Usually we still find in the hind wings of the Libellulidæ
two longitudinal veins, still quite distinct, which arise from
A₁. As we find the suggestion of a fusion of the two longi-
tudinal veins with A₁ in the "Protodonata" also, the con-
ception of the composite nature of A becomes possible.

We did not finish the investigation of Cu and the triangle.
The triangle represents a frame which presses apart and at
the same time strengthens Cu and M. The perfection of
this frame in the Anisoptera evidently becomes an acquisi-
tion of importance and use in the mechanism of the wing.
We find the formation of the triangle in the Archithemidæ
and Heterophlebiidæ in statu nascendi. Its forms here
were rather diverse, sometimes different in the fore and
hind wings, and in general these triangles did not corre-
spond entirely to the triangles of the Anisoptera. These
groups with the aberrant triangle died out, and only the
groups with the normal triangle were developed and became
preserved up to the present time. In the series of Aniso-
zygoptera-Zygoptera no triangle was formed, but in con-
nection with this the original form of the wing is also not
preserved, the venation, changed greatly in the anal area,
became reduced, Sc became shorter, etc. But originally,
as we notice in the Lestinæ and in the related Anisozygopt-
tera, the distinct projection of Cu (and A₁) was here also.
The same kind of projection is also clearly expressed in the
very conservative group Ephemeroidea Ulm. The triangu-
lar area between the bases of Cu₂ and Cu₁ in the families
of this suborder also closely resemble the triangle in the
dragon-flies, only its external side in the former is repre-
sented not only by one straight vein, but by two cross-veins
(between Cu₁ and Cuad, Cu₂ and Cuad), which are sel-
dom placed opposite each other. The "inserted sector" Cuad
is also often found in the Anisoptera; it is also well repre-
sented in the fossil Heterophlebiidæ by a longitudinal and usually uneven vein anterior of Cu. All these comparisons lead to the conclusion that in the dragon-flies, Cu₁ of the authors is not at all Cu₂, but that it corresponds to Cu₂ of the may-flies. Cu₁ of the may-flies does not exist any longer in the dragon-flies.* It is very possible that Cu₁ of the may-flies is CuA₁, but at present we cannot ascertain this.

The top side of the triangle was formed, according to Needham, by a cross-vein between Cu and M, slanting distally. This is contrary to certain facts. In Neurothemis oculata Fab., for instance, and even more in Aeschnidium, the region of the triangle, as well as other areas, is occupied by a thick net and between M from one side, and Cu and the top side of the triangle from the other side, is distributed a thick series of short cross-veins. It is absurd to attribute the formation of the upper side by an inclination of a cross-vein. The outside as well as the upper side very likely was crystalized, as it were, directly from the network (certainly of very fundamental origin) under pressure of mechanical causes. Furthermore, this vein exists in order to join the basal part of Cu with M. If it came into that position by the slanting of a cross-vein (between Cu and M) one would not understand how it could pass by M and terminate on the exterior side of the triangle, a short distance down from M; this condition one encounters sometimes in the Libellulidæ and we find it in Heterophlebia, where it goes to the exterior side and is almost parallel to M (hind wing, H. dislocata). Such diversity points to the diverse nature of the formation of this vein. As soon as this wing-structure, which was derived from the configuration of the venation and of the wing form and for the working of its parts, acquired the formation of a triangular frame, its two sides (the interior side is formed by the downward projec-

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* At the request of Dr. Martynov, the following sentences, which were in the original, have been omitted: "In the Protodonata (Mega-neura, Boltonites, Typidæ) we also usually find the simple anterior branch CuA₁, and the branch CuP joined to the anal group. This seems to point to the conclusion that Cu₁ of the dragon-flies is CuP, and that CuA disappears in them."
tion of Cu) begin to form themselves from the veins existing there, no matter which ones. It seems to be not an impossible idea that the upper side in some groups could be the remains of the original part of Cu₁. Cu₁, as in the may-flies, had to be concave, and this top side is concave, changing at the end into a sharply convex M. The fact that its end does not reach M would therefore be comprehensible. On this theory I do not insist because I cannot offer any definite facts of proof.

In the Zygoptera the true triangle does not exist, but in the Agrionidae—and they form the main part of the Zygoptera—a structure was formed which in its function, to a certain degree, replaces the triangle. This is the "quadrilateral," which hereafter takes the form of a narrow triangle. It is very certain that such a structure as it is represented in the Lestinae, for instance, does exist, and is indicated by the fact that from the Anisozygoptera up to the present time only such a form as (Epiophlebia suprestes Selys) was preserved, where the "quadrilateral" has a form identical with that in the Lestinae. Where the projection of Cu was not fixed by the formation at this place of the frame of a triangle, or quadrilateral of the type of Lestinae, there the existence of this projection, and below the projection of A₁, lost its mechanical significance. More than that, this projection because of the functioning of this vein would be entirely without purpose and even harmful. It is not surprising, therefore, that in the Calopterygidae, where the "quadrilateral" did not adopt the form as in the Lestinae and Epiophlebia, Cu tended to straighten itself out in diverse ways; a tendency which reached its maximum development in Calopteryx and related forms.

Preceding the above discussion, I compared the venation of the dragon-flies with the venation of the Carboniferous Protephemeroidea (Trilolsoba) and through them to the Dictyoneuridae. I referred little to the Protodonata because the evolution of their wings was along different lines from the dragon-flies. It is true that in part of them two branches of M are represented as well as the two branches of Cu, which do not exist in the Odonata; but in other respects they are more specialized and go further than the dragon-flies from such groups as the Dictyoneuridae. One
can say that the primitive net of their wing was used for the formation of secondary longitudinal sectors, which imitate and take the position of the original ones. In contrast to what was as a rule expressed in the evolution of the Palæodictyoptera, may-flies, and dragon-flies, Rs did not expand, but decreased. In these the distribution of branches of Rs and also M₁ and Cu is more pronounced than in the Odonata, and departs from the distribution which we find in the Dictyoneuridae and Protephemerioidea. In this respect the Odonata have preserved more of the primitive features. The one-sided and extreme specialization of the wing venation of the Protodonata, with the loss of some fundamental features of their ancestors, were probably one of the main causes which brought about the rapid extinction of the group.

From the base of the Odonata there separated off, probably some time before the adoption of the main features of the recent venation, one more group known to us through a single representative from the Liassic—Protomyrmelon brunonis Geinitz. The wing venation of this form was figured by Handlirsch on Pl. 42, Fig. 14, and is reproduced here in Fig. 8. Some superficial resemblances with the Zygoptera, and at the same time some singularities of venation, lead the author to isolate the species in a separate sub-order, Archizygoptera. Sc is very much shortened and Rs and M very strongly distorted, so it is difficult to understand their distribution. Handlirsch represented Cu as two-branched; below it came the anal. If Cu is actually composed of two branches, then this fact, together with the peculiar structure of RS and M, would be sufficient for us to place this form into a separate order by itself. But one should note that the base of the wing is not well preserved in the fossil.

Now let us look briefly at the tracheation of the wings of the may-flies and dragon-flies. Such an inquiry is natural. If our interpretation of the venation of the dragon-flies and may-flies is correct, how can we explain, then, the way the trachea of RS runs in the anisoptera, where the trachea which arises from R is opposite the nodus, crosses RS₁ and RS₂ and enters into the vein RS₄, extending, and often a great deal, from its base? How can we explain the almost regular
absence of the trachea in RS4 of may-flies, and also of a series of distal branches chiefly convex, as in Agnatha, Odonata, etc? Let us try briefly to throw some light on the question; and let us start with the may-flies.

A characteristic feature of the tracheation of the anlage of the nympha! wing\textsuperscript{12} appears to be its exceptional diversity in different groups and its marked instability, which is shown in a very great individual variation. By studying the tracheation in different groups and comparing it with the venation, we observe in the diversity a definite correlation with the peculiarities of venation. I base this statement upon the work of Morgan, who gave a series of illustrations of the tracheae of nymphs of different may-flies, as well as on my observations. Only in some of the more primitive forms and then only in the early stages of the development of the wing anlage, do we encounter, as shown by Morgan, in Chiratonetes, for example, the normal full tracheation, with the penetration of the tracheae into all longitudinal veins through their bases. In the later stages of development of the same Chiratonetes the part of the trachea which goes into RS\textsubscript{1} (=M\textsubscript{1} Morgan) disappeared and instead of this a series of small tracheae was directed into the vein RS\textsubscript{1} from the neighboring, stronger trachea R. A quite full tracheation exists according to Morgan in Heptigenia sp. (P. 5, Fig. 3), but here the tracheation in RS\textsubscript{1} and also in some other small branches has already disappeared. I repeat, we seldom encounter normal tracheation. In most of the may-flies we usually encounter a regular alternating of veins in which the tracheae normally penetrate through the bases with veins which have no such tracheae, and which are tracheated by numerous small branches from tracheae of the neighboring veins (see e. g., Fig. 11, which illustrates the course of tracheation as in species of Heptigenia Ulmer). Almost always the vein (with a few known exceptions in Cheratonetes and Heptigenia) which is tracheated

\textsuperscript{12} If the tracheoles are distinguished with difficulty in the wings of the imagines of dragon-flies, then it is still more difficult in the may-flies. However, the characteristic features of the venation and tracheation of the adults are already indicated in the nymphs, and for that reason we shall investigate the imagines instead of the nymphs.
by such means and which was one of the first to lose its own trachea, is RS₄ (=1 Morgan); that is the vein which has no normal tracheation in Odonata, where it receives the trachea either from RS₃ (Zygoptera) or from R (Anisoptera). Furthermore, the convex vein between RS₁ and RS₂ is tracheated (almost exclusively) in the same way. Tracheæ which go into M and R are often very weak also, or even vanish entirely (especially in M), and in such a way these veins adopt a secondary tracheation from the branches of the neighboring trunks. The intercalary vein in Cu₁ is similarly tracheated, sometimes A₁ also. If we compare such characteristics of tracheation with the characteristics of venation, then without effort we shall notice the fact that the first veins to lose their own trachea and begin to be tracheated by small branches from neighboring trunks are all veins which were made "inserted" (independent, intercalary, Shaltsectors, etc.), —that is, which lost their origins. Such veins as far as known are almost always convex veins. Furthermore, in the more primitive species groups as Bætoidea, but also Siphoneuridæ and a few Ephemericidæ, the tracheæ which go into M and R, that is already into the main but exclusively convex veins, are weakened and eventually disappear. We have said above that because of this loss and even by the weakening, of trachea as in the case of R and M, which penetrate into the vein through the base, this vein begins to be tracheated by small branches from the neighboring tracheal lines. The tracheation of such "inserted" veins is, however, very diverse, because branches penetrate into it not only from neighboring systems but also from trunks which lie further away anteriorly and posteriorly. Such small branches must quite often go a long way around before they come into the necessary vein. Quite often some small tracheal branches, which are derived from the neighboring trunks as well as the trunks placed further away, become a great deal stronger than others, and accept the chief burden of tracheation; in such cases one or the other part, and sometimes most of the small tracheal branches, are subject to reduction. Finally, not rarely there are cases when only one trachea receives the repossessions and tracheates almost entirely a given vein (a certain part of the
small branches or neighboring trunks nevertheless remain). The methods of tracheation, as it was noted above, are very diverse in general and subject in particular to a strong individual variation. The one or the other vein is tracheated sometimes only by small branches, sometimes also by larger ones. The latter penetrate either from the nearer or from the further lying trunks, etc. Evidently a series of causes not considered here (that is, certain circumstances), influence the distribution of smaller branches. Sometimes, however, the one or the other method of tracheation is understandable. In a number of forms, as noted, the trachea RS does not continue into the distal branch RS1, but turns off into RS3, and RS1 is tracheated by small branches. This we will understand if we remember that alongside RS there runs the trachea trunk R, which can supply RS1 with branches. However, when R disappears, the trachea RS1 is usually preserved. Morgan, seeking for an analogy with the dragon-flies, noted that in one species of Heptigenia and only in part of these specimens, the tracheae which supply RS3 (=RS? Morgan) separate not only from the trunk RS, as usual, but also from R. Desiring to see in this analogy with the Odonata, Morgan concluded that this vein is Rs, and that here we have a preservation of the crossing of the tracheae and veins, which sometimes took place in the may-flies and now in dragon-flies. It is not necessary to say that such a conclusion, which is now supported by Comstock (3), has not enough foundation. In all may-flies the concave RS3 is tracheated in a normal way from a concave trunk RS (=M1 Morgan and Comstock), as it should be, and only in part of the specimens of Heptigenia studied the strongest trachea appears to be a branch of R. Taking into consideration the unusually great amount of variation in general, and the capriciousness of the tracheae, can one attach such great significance to this exception, and conclude that this condition once existed in all may-flies, i.e., that in all may-flies RS takes root in the region of the media? Evidently such a con-

13 Only in the Anisoptera. Morgan says that the crossing was unquestionably present in the Zygoptera, but that is pure hypothesis which has no supporting facts and is more than doubtful.
clusion is very daring and was prompted by the wish to find a full analogy. However, Morgan is wrong in supposing that by such an interpretation a full analogy with the dragon-flies is established, because RS of the may-flies is a concave vein and corresponds completely to a concave vein in the dragon-flies, i.e., to RS₃; but not to the convex vein, RS₁, which almost always has the character of a “Schaltsector,” and which, according to the understanding of the authors is a branch of R₁, i.e., RS. To this vein there entirely corresponds in the may-flies another convex vein, also always inserted, which Morgan indicated as I and Comstock as IRS (intercalary). If one attaches importance to such exceptional cases of the entering tracheal trunks, then we lose any support of the theory of the establishment of homology of the veins. According to the illustration of Morgan (Pl. 5, fig. 7) in Epeorus humeralis, the vein 1 is supported in the distal part by one trachea from M₂. Why in such a case should we not consider vein 1 (that is, RS₁) to be only the branch of M₂ (that is, RS₂) and its basal part as a bridge? In Blasturus, according to the same author (Pl. 6, fig. 27), the middle (interia) vein of the media is tracheated by one trachea which separates from RS₃ (=M₂ Morgan). Why not suppose that the crossing once existed here, and not consider that this vein is a branch of RS₃, etc.? Such a supposition is not more unlikely than the one assumed by Morgan.

I have already noted above the fundamental nature of the relationship between the tracheation and the character of the venation. Those veins which have lost the normal method of origin from other veins and become “inserted sectors,” that is, after weakening at the base, have lost the base itself, those veins have lost the normal mode of tracheation and acquired a secondary tracheation. Such veins are the convex branches and also some small secondary, distal, concave branches. It is true that not everywhere the convex vein-branches changed into “inserted sectors”; there are exceptions, though very seldom. Thus in Palingenia, RS₄ in the fore wings¹⁴ originates nor-

¹⁴ In the hind wing this vein is already a typical inserted sector.
mally and has not yet changed into a typically inserted sector. Nevertheless, here this vein takes a definite convex position and forms at its base a projection towards the concave vein R. This is sufficient for the secondary tracheation to be adopted. The main convex veins, R and M, had originally and have still in many species their own tracheal trunks, which penetrate into them; but in the other weaker tracheæ and in the more specialized groups, as in Bætoidea, for example, where the membrane is very fine, all superfluous veins are discarded and in the remaining ones the alternation of convexities and concavities is sharply expressed up to the very base, where the main convex veins, R and M, lose their own tracheæ.

The indicated relation becomes clear to us, if we look at it from an historical point of view. There was certainly once a time when the alternation of convex and concave veins was only suggested. There was still no inserted sectors, and the present convex RS₁ and RS₂ of recent types had a normal origin from R. Because of the absence of plaiting of the wings and the diversity in the methods of origin of the different veins receiving the trachea normally (that is, through the base from larger trachea of other veins of which they were branches), this position of the tracheation is approximately preserved at the present time, as mentioned above, in a great many primitive forms, and also in the earliest stages of development of the wing anlage in nymphs. As the wings “mechanized” more and more, that is, as the membrane became finer, the veins adopted an alternation of convex and concave positions, the basal part of the veins at the time of the change from the concave position (e. g., of R to RS₁) weakened and finally was obliterated. The normal tracheation through the base into the convex vein became more and more difficult, and then became impossible, when the vein

35 By this I do not mean to say that all, even the smallest irregular distal veins, were originally normal branches which arose from other veins. Small branches were formed at their places from the primitive network, were unstable, irregular, diverse and as a rule gave rise to no (secondary) alternation of convexities and concavities. Now, as before, they are tracheated by small branches probably in very diverse ways. These supplementary, secondary veins I do not consider here.
lost its base. This condition was carried over into the nymph, where in general there was at once laid down the foundation of imaginal venation. Such convex veins had to acquire a small tracheal supply by some other means. The small tracheoles in may-flies and dragon-flies (in nymphs and young imagines) frequently separate from the longitudinal trunks, and by means of the cross-veins usually reach the neighboring trunks. When the basal tracheal trunks began to weaken the small side branches of the neighboring trunks began to strengthen in their place, and finally to replace them completely in function. Because of causes which we cannot consider further, one or the other branches strengthened to the disadvantage of the others; and sometimes the tracheation, chiefly in one trachea which arose either from a neighboring or a remote trunk, appeared to be the most preferable. Since the strengthening of some of the small tracheae depends upon a thousand small causes, because of their multitude and original similarity, even in the development of one individual, it is natural that the secondary tracheation had to be a very diverse and variable one. Under such conditions in the interpretation of the venation one should not attach any importance to the fact that in a certain species a vein receives its secondary tracheae from neighboring trunks and not from the side where it should be. Such appears to me the origin of the secondary tracheation of may-flies; and if this idea is correct for the may-flies, then it is also correct and entirely applicable to the dragon-flies.

In dragon-flies the whole character of the tracheation of the wing in its relation to the venation maintains in general the same character as in the may-flies, since the dragon-flies have much less diversity and much more stability in tracheation than the may-flies. The tracheation of R is preserved everywhere, which is comprehensible to a certain degree if we consider the shortening of the subcosta in the dragon-flies. The tracheation of M is also preserved, although in the Zygoptera it is sometimes greatly weakened. The convex RS₂, RS₄ and A₁ obtain a secondary tracheation by small branches from the neighboring tracheae; the cross-tracheae are of course supplied by the small supplementary distal, longitudinal veins. The media
in the Zygoptera is supplied by its own trachea as well as, to a greater or less extent, by the small branches of the neighboring veins. RS2, together with a series of other veins in the region of Rs and M, are supplied by small tracheoles (see fig. 9), but in Zygoptera the vein RS4 is tracheated in this way at its basal part, while in its distal part usually (but with exceptions) by one fairly large branch which arises from RS3 (fig. 9). In the Anisoptera, this same RS4 receives its trachea from R1, and even the basal part of this vein (the “bridge”) is tracheated chiefly by the branch of the tracheae directed posteriorly. Comstock and Needham conclude from this fact that the vein RS4 is actually RS, which takes root in the region of the media; and they extend this conclusion to the Zygoptera, in which this type of tracheation of RS4 was never observed. From my historical point of view, such a tracheation of RS4, and in particular the difference in both suborders, becomes generally clear. The convex branches of RS and also A1 for the same reasons as in may-flies lost their original and normal mode of receiving tracheae and acquired a secondary tracheation at the expense of the ever-increasing small branches from the neighboring trunks, which used to enter here before. Such a method of tracheation was preserved in the basal part of RS4 in Zygoptera, but in the greater distal half one treachea which separated from RS3 became predominant. This acquisition of predominance by one or several branches in dragon-flies as well as in may-flies, is often found in the distal longitudinal veins, and there is nothing surprising that one of the tracheae strengthens at the expense of the other in RS4. Originally, when the present-day type of tracheation was only beginning to evolve, the greater diversity probably took place here, as in the may-flies. Having lost its tracheation, Rs4 received at first the tracheoles from the neighboring trunks as well as from R, and in the same group some tracheal branches obtained predominance; and in other groups, other branches, etc. The tracheation of RS4 in the Anisoptera from R was at last established (why, is another question); in Zygoptera, partly from RS and partly by the mere preservation of an earlier means of supply by small tracheoles (in the basal half). It is difficult to say why the tracheation of
RS₄ by the branch from R or RS₃ (almost) was established, but I think that the formation of a stable point of supply at the nodus had great influence upon the process of acquiring such a tracheation. In the Anisoptera the point of origin of the branch in RS₄ from the trachea R is just opposite the nodus. In the region of the nodus the wing is certainly stronger, is much less able to bend, and is much less exposed to occasional deformation at its distal point. The trachea which arises from this place in R is naturally more protected at its base and therefore more able to be strengthened and preserved than other more distally lying branches from the neighboring trunks. In the Zygoptera RS₄ is supplied by an entirely different trachea; this is from RS₃, but here also the place of origin of the trachea is opposite the nodus, though a little more distal. However, one should bear in mind that in the evolution of the Zygoptera, there took place migration of the nodus towards the base, so that the separation of the point of origin of RS₄ and the nodus becomes clear. The difference between these suborders in the tracheation of RS₄ proves my supposition about the original diversity and the probable variability of the growing secondary tracheation in the dragon-fly. It would be strange if in both suborders, which are so different on the basis of their venation, there should have been established a similarity of RS₄.

Unquestionably the tracheation is also secondary. This tracheation in general is similar in both suborders, but there are a few which are somewhat inconsistent. The tracheation of the wings of dragon-flies differs in general from that of the may-flies in its stability; but the stability is not so great as one would think and one encounters in the Anisoptera, a variation of even a serious character. I did not investigate these questions specifically; I shall mention only four young nymphs of Aeschna sp., which were taken together in the fall of 1923 in a little pond near Lakhta; in one of these the tracheae appeared to be anomalous in the following features: in the left fore wing the trachea R behind the nodus gives rise to a strong trunk, which at once separates again into three branches, entering into RS₄, RS₃ and RS₁. Only RS₅ is tracheated here from the trachea of the media. In the right hind
wing the trachea which supplies our M (M of the authors), appears to be free up to the very base, and arises only very near the trachea RS (fig. 12). The last variation is especially interesting as indicating that the origin of the trachea M from the general trunk Rs,M is perhaps the result of a secondary fusion of the base of the trachea M with the base of RS.

And so the investigation of the tracheation of the wings of dragon-flies and may-flies from a functional and historical point of view leads us to the conclusion that the peculiarities were developed in connection with the acquisition of the characteristic features of these groups, the alternation of convex and concave veins, and usually the change of convex ones into "inserted sectors." Such features are characteristic of these two recent groups and the related fossils, Triblosoba, Protodonata (in part), some Megasecoptera and evidently some Palæodictyoptera.

The study of the relation of the jugal areas to the remaining part of the wing lead me in another work (7) to the conclusion that the Insecta Pterygota probably separated during the Lower Carboniferous into several branches which went along different lines of evolution, the Paleoptera (Paleodictyoptera, Megasecoptera, Agnatha, with their Carboniferous relatives) and the Neoptera (the remainder of the Pterygota, which at rest fold their wings roof-like over their abdomens). My study of the venation and the tracheation of the wings of may-flies and dragon-flies proves this conclusion, because according to the wings both these groups are similar in many ways to the Dictyoneuridæ, Triblosoba, and the typical members of the Paleoptera.

In conclusion, I would like to discuss one more question. How can one explain that out of the once rich and diverse group of Paleoptera, there are now existing only the Agnatha and the Odonata, the other groups having died out? I think that in a discussion of this question we should not forget the structure of such an important organ as the wing.

Of course the wings of recent dragon-flies are much more perfect than those of their remote ancestors, which were like the Dictyoneuridæ. They have lost most of those veins of their ancestors which were unnecessary from a
mechanical point of view (among the even the main branches of M and Cu); they have changed their form (may-flies) and have acquired (dragon-flies) such important mechanical structures as the triangle and the parts adjacent to it, that they have in general become greatly mechanized; but by this means we hardly can explain the persistence of these two groups, because the wings of many extinct groups had also attained that mechanical perfection, particularly the Megasecoptera, Protodonata, and many groups and families of the Palæodictyoptera. The Megasecoptera, as well as the other groups mentioned, advanced very far, but nevertheless died out early. Evidently all this explanation is insufficient and something else is needed. Comparing the wings of may-flies and dragon-flies with the wings of the most primitive forms, e. g., Dictyneuridae from one side, and from the other side the Megasecoptera, Protodonata and more specialized Palæodictyoptera, we find, between the one and the other, distinct differences. In the Megasecoptera the venation is so much reduced that their wings resemble those of the Dictyneuridae only slightly.

In the Protodonata the number of longitudinal veins, on the contrary, has increased greatly, but the relative dimensions of the systems of Rs, M and Cu, and the distribution of their branches have greatly departed from that which we have seen in the Dictyneuridae. Similar changes in dimension and distribution of branches are encountered in many Paleodictyoptera. Dragon-flies (especially Anisoptera) and may-flies, on the contrary, differ in that, disregarding the various specializations, they preserved the original relative dimensions of the systems of the main veins and the distribution of branches (especially Rs!). The Anisoptera preserved their primitive form of wing. Such preservation of the fundamental primitive features was the reason why the specialization of the wings of dragon-flies and may-flies did not become fatal for them, as in the case of the former groups. A too rapid specialization, with the loss of the original primitive features, as we have in the Megasecoptera, Protodonata, etc., inevitably narrows greatly the potentiality of further evolutionary modifications, and leads such groups to an end of development and
consequently to extinction.

And so this study of the venation of the two recent orders, the Agnatha and the Odonata, which to my mind represent the branches which separated early from the more primitive forms of the very similar Dictyoneuridæ, and which have nothing in common with the Neuroptera and Plectoptera\textsuperscript{16}, leads me to the conclusion that such characteristic features of the venation and the distribution of veins (in particular RS, partly M) of the Dictyoneuridæ were preserved better in the dragon-flies and may-flies than in many Palæodictyoptera or Megasecoptera, in which the venation was too specialized or too reduced. May, 1923.

P. S. My work was already in the press of the Russian Entomological Review when the July number of Psyche (30: 1923, nos. 3-4) appeared, with an article by Aug. Lameere on “The Wing Veins of Insects.” In this small but very valuable article, the author discusses chiefly the venation of the Palæodictyoptera, the dragon-flies and the may-flies, and in many respects comes to the very same conclusion on the question of the interpretation of the venation as I have.

In the treatment of RS in the dragon-flies and the may-flies we agree perfectly, aside from terminology. According to Lameere, also, the media of may-flies corresponds to the posterior branch (our MP), in Triblosoba, etc., and the media of the dragon-flies according to the author is MA (my terminology). From a comparison of the Protodonata, I now entirely share this interpretation, according to which the dragon-flies lost MP. In the treatment of the cubitus we do not agree in everything, because the assertion of Lameere that the may-flies, as well as the dragon-flies, have lost CuA, is to my mind not entirely proven. I will not discuss here the venation of the other groups, and will note only that the conception of the author that there is a close relation between the Hemiptera and the Palæodictyoptera appears to me unlikely. According to my understanding of the venation of Eugeron, it is constructed entirely after the type of the Palæodictyoptera, and is far from the type

\textsuperscript{16}The Plecoptera have to be included according to my understanding into the super-order Orthopteroidea. A similar view has been taken by Lameere (1917).
of the Hemiptera. Eugereon, together with several other forms, represents only one on the branches of the Palæodictyoptera, and one can hardly connect it with the Hemiptera, which represents an entirely different trunk and must be referred to my group Neoptera; the latter separated very early from the division Paleoptera, to which one should assign Eugeron Dorhn. To all these questions I hope to return. Fall, 1924.

REFERENCES


EXPLANATION OF FIGURES

Fig. 1. Wing (hind?) of Polioptenus elegans Goldenberg.
Fig. 2. Fore wing of Eumecoptera laxa Gold.
Fig. 3. Wing of Triplosoba pulchella Brongn.
Fig. 4. Wings of Hexagenia bilineata Say.
Fig. 5. Fore wing of Gomphus descriptus.
Fig. 6. Basal part of hind wing of Heterophlebia dislocata Brodie and Westw.
Fig. 7. Base of hind wing of Phylopetalia apicalis Selys.
Fig. 8. Wing of Protomyrmeleon brunonis Geintz.
Fig. 9. Tracheation of wing of nymph of Lestes rectangularis Say.
Fig. 10. Hind wing of Palingenia longicauda Oliv., after Eaton (5).
Fig. 11. Tracheation of the anlage of the fore wing in the adult nymph of a member of the Hexagenioidea Ulm. (original).
Fig. 12. Anormalous tracheation in the hind wing anlage of a nymph of Æschna sp. (original).

Figures 1, 2, 3, 6, and 8 after Handlirsch (6); Fig. 4 after Needham (8); Figs. 5, 7, and 9 after Needham (10).
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