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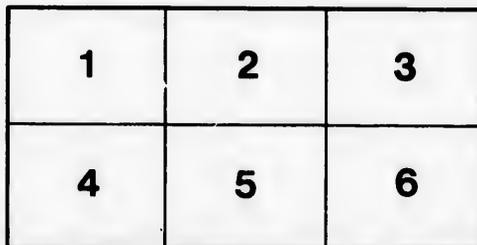
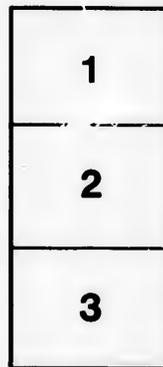
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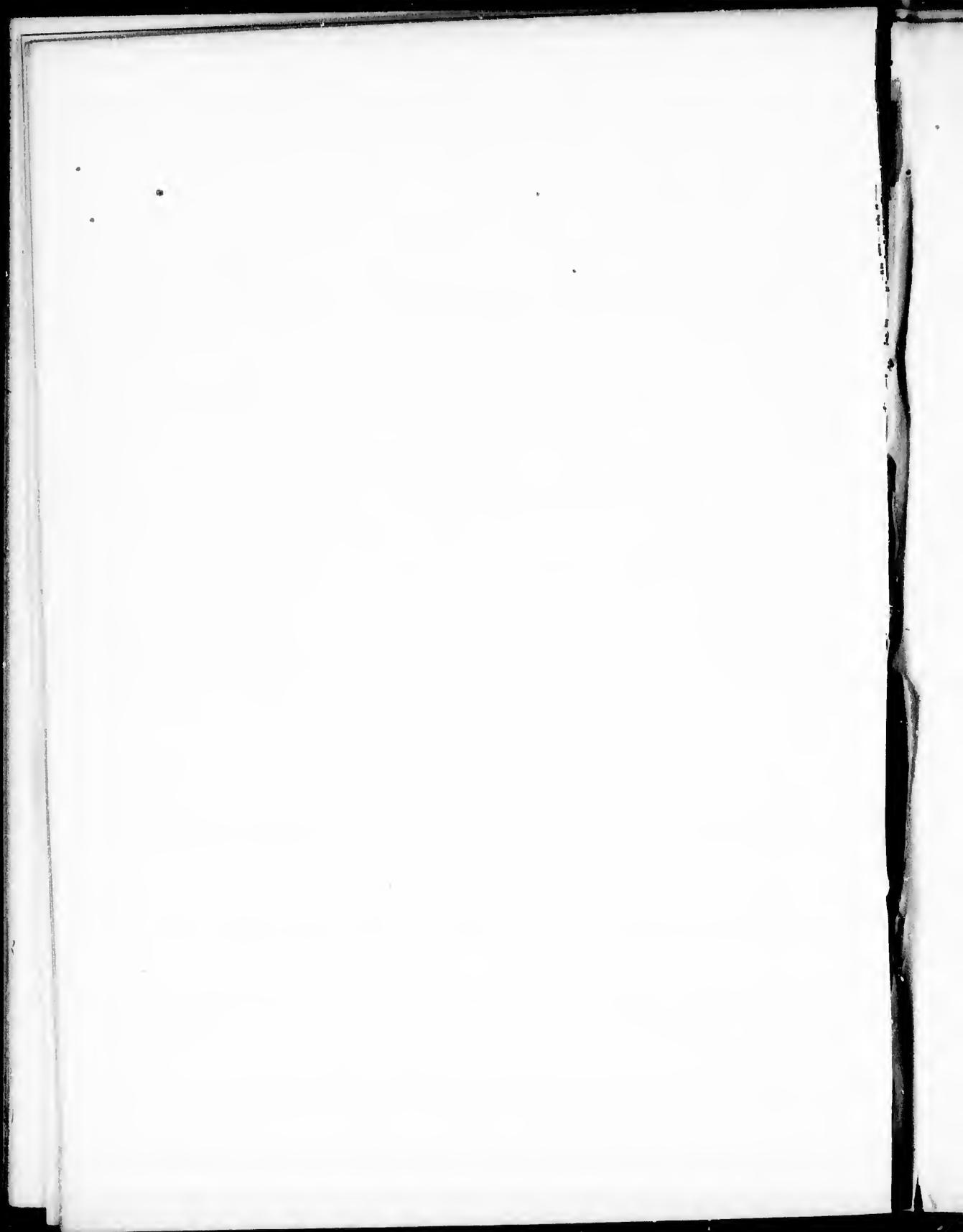
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THE EARLIEST WINGED INSECTS OF AMERICA: A RE-EXAMINATION OF THE DEVONIAN  
INSECTS OF NEW BRUNSWICK, IN THE LIGHT OF CRITICISMS AND OF NEW  
STUDIES OF OTHER PALEOZOIC TYPES.

**B**ELIEVING that science is little advanced by the acrimony engendered by controversial essays, the writer has always avoided replying to any criticisms of his scientific work, however destructive they might appear at first sight, until in the natural course of subsequent studies it became necessary to subject them to public examination. Generally much time will then have elapsed, both parties may view the matter more dispassionately and, notwithstanding the delay, the truth is likely to be sooner reached.

It is on this account that up to the present time I have in no way noticed the objections which Dr. Hagen<sup>1</sup> made four years since to my interpretation of the wing-structure of the Devonian insects, although his criticisms were not always couched in the most temperate language. Now, however, that it has become necessary, for a work in hand, for me to review systematically the entire series of paleozoic insects, the Devonian wings have been studied anew, with the intention of profiting by the comments of so thorough and learned a student of Neuroptera, both recent and fossil, as Dr. Hagen is everywhere well known to be; of profiting also by the greatly extended special knowledge I have myself gained in the last five years through the kindness of many correspondents (and especially of Mr. R. D. Lacoe), who have liberally furnished me with a very considerable number of new paleozoic insect types, discovered in this country.

Without wishing to discredit in the least the worth of Dr. Hagen's general opinion in questions which affect the Neuroptera, I think it is only fair to point out dispassionately to the inquirer of the future four things. 1°. That in the historic development of the broader groups of insects, so far as we now are acquainted with them, no important changes have transpired *since* paleozoic times; while our perplexity regarding the proper relation of paleozoic insects to modern types is often very great, and our conclusions variable. 2°. That Dr. Hagen has published nothing upon paleozoic insects (apart from the paper above referred to upon Devonian insects) excepting scattered notes on a few which he referred to Termitina and which, in all probability, are no Termitina at all.<sup>3</sup> 3°. That there is no evidence, but the contrary, that Dr. Hagen in his investigations, *uses* the "theory of descent" as a working hypothesis, without which no one who is studying any group of animals in the period of its rise and most rapid evolution can expect to do otherwise than stumble and wander astray. To refuse to use it is to merit failure. 4°. That

<sup>1</sup> Bull. Mus. Comp. Zool., VIII, no. 11.

<sup>2</sup> Anniv. Mem. Bost. Soc. Nat. Hist., 1880.

<sup>3</sup> See Proc. Amer. Acad. Arts Sc., XX, 167-173.

of the Devonian wings, Dr. Hagen has studied in nature only the (in most cases poorer) reverses of the original specimens, while several times before and once since the publication of his criticisms I have carefully studied both sets together.

***Gerephemera simplex.***

This insect was placed by me in a distinct family group to which I gave the name of *Atocina*. Comparisons were particularly instituted with one of the other Devonian forms, *Platephemera*, and with *Dietyoneura* and its allies of the carboniferous epoch, to the latter of which it was thought to have most resemblance. At that time the gigantic forms of *Protophasmida* made known by Brongniart had not been published, and I was not aware of the variety of venation found in that ancient type. Now that this is known I am far more inclined, notwithstanding its anomalous structure, to believe that *Gerephemera* should fall in the same general group, and that the name of *Atocina* should be dropped; particularly as a new study makes me see that the venation will bear an interpretation which lessens the points of distinction between them, and renders the structure of *Gerephemera* less anomalous.

Dr. Hagen, on the other hand, refers it unhesitatingly to the modern Odonata; but a certain part of my description has been plainly misunderstood by him. The costal margin is represented both in the description and in the figure as two to three mm. long; in the figure it is not eight mm. long, as stated by him. I have not said that "the mediastinal vein is never a depressed one in such insects," but "the marginal would then be an elevated and the mediastinal a depressed vein, which [combination] is never the case," etc. He rightly says that no mention is made of the quadrangular cells occurring between the oblique nervules which run from the mediastinal vein to the margin, for they were not looked upon as important and are exceedingly faint and obscure. He remarks that if they exist they would be the only features inconsistent with an Odonate hypothesis, overlooking the fact that the nervules they are supposed to connect are strongly oblique, as never in Odonata and usually in other Neuroptera. The superior origin of the branches of the principal vein preserved, which he calls "probably the sector medius," is also entirely inconsistent with an Odonate hypothesis, and is the most salient point in the wing next to the numerous parallel veins above it, but to this he does not at all refer.

The superior origin of the branches of this vein, however, is not unknown in paleozoic wings as I had supposed, having its counterpart in several of the *Protophasmida*, as Brongniart calls them, and I am now inclined to believe that this wing should find a place here, somewhere in the neighborhood of *Haplophlebium*. This would necessitate a different and I think a somewhat more rational view of the venation, viz., that what I had looked upon as the externomedian is the internomedian vein, and that the externomedian is the first branched vein in the wing, counting from the costal border, the "intercalary nervure" being really a branch of this, room for other branches being found, if the main externomedian branch felt the curvature of the apex of the wing as soon as the other veins; this would bring the slight bend in the outline of the outer border at the extremity of the outermost anal vein (so frequent in insects), but would give an enormous expansion to the anal area, as in the case in some other paleozoic insects and as occurs in several of the *Protophasmida*, especially in the neighborhood of *Haplophlebium*.

Dr. Hagen examined the reverse of the principal specimen, and says of it, it "strongly confirms my determination." "It belongs," he says, "to a part of the base of the wing which is not preserved" in the figure published. It shows, according to him, the "sector trigonuli inferior," which belongs to the base of the wing and "is to be found only in Odonata, never in Ephemerae." Unfortunately for all this, the reverse, now figured for the first time (in reverse) on fig. 9 of the accompanying plate, is the exact counterpart of that portion of the better specimen (of which a figure was published in my former paper), which lies *farthest* from the base of the wing, and a piece of which is poorly figured on our present plate at fig. 8 (again in reverse). As I have had both obverse and reverse to compare both before the larger part of the better specimen was uncovered, again after that addition to our knowledge, and still again for verification since the comments of Dr. Hagen, this point cannot be disputed. It will be observed that in no other place is Dr. Hagen's language more positive than here.

#### **Platphemera antiqua.**

This insect was referred by me to the Ephemerae, because the venation "agreed in all essential features with that family, and . . . considering the antiquity of the creature shows marvellously little divergence from living types." Its relation to Dietyoneura and allies was discussed, and a "general similarity" of structure pointed out, though they were not considered "closely affiliated."

Dr. Hagen, on the contrary, states that it "has nothing whatsoever to do with the Ephemerae," adding that his "deliberate determination is not based upon a difference of opinion, but merely on the simple evidence of facts." The specimen is a part of the apical half, without the tip, of a wing of a gigantic dragon fly.

Recognizing the life long labors of Dr. Hagen upon the Odonata, the writer has striven earnestly to see this fossil in the light in which Dr. Hagen declares that he sees it, but is obliged to confess that the distortion is not within his power. The "simple evidence of facts" is unalterably opposed to it, as the following considerations, among others, seem to show, in which the special points of Dr. Hagen's assertions or criticisms are touched upon.

1. In no dragon fly, living or fossil, is there found, beyond the nodus, between the "mediana" and the margin, more than a simple longitudinal vein—the marginal vein; excepting close to the nodus, where the subcosta sometimes appears to extend a very little way beyond the nodus, and then terminates *on the mediana*. In *Platphemera* there is an additional vein, which, on Dr. Hagen's hypothesis, extends much more than half way from his location of the nodus to the tip of the wing, and terminates *on the marginal vein*; in other words, there is no nodus,—one of the chief characteristics of Odonata, absent, so far as I know, from no dragon fly, living or extinct.

2. To carry out this hypothesis of an Odonate structure, Dr. Hagen is compelled to say that "something less than 20 mm. of the tip are wanting." To add only 15 mm., as is done by the dotted lines in the accompanying sketch, would, on the most favorable showing, make a wing of ridiculously extravagant appearance; the course of the known portion of the lower margin will not allow us to suppose, at the outside, more than 5 mm., and probably not more than 2 mm. of the tip to be lost.



Tip of wing of *Platphemera*, restored by Dr. Hagen's data.

3. The narrowing of what Dr. Hagen calls the "second cubital space" is a common feature in Ephemeridae (e.g. species of Calliareys, Choroterpes, Blasturus, Atalophlebin, Rhoenanthus, Chloeon, etc.), though not often to quite such an extent, nor perhaps quite so rapidly, as here; and as this varies in different species of the same genus, it seems to be a very unimportant matter; the approach of the two veins, contrary to Dr. Hagen's statement, is mentioned in my paper.

4. What Dr. Hagen calls the sector subnodalis does not run unbroken to the tip, as in all dragon flies I have examined, but is lost in the reticulation shortly before the margin.

In looking over all the ancient types known, I find none to which this insect may be at all closely compared excepting the Ephemeridae; unless it be Breyeria, to which it bears some distant resemblance, and to which it is not impossible that it is allied; but it differs strikingly in every detail from that form, and so much more closely resembles the Ephemeridae of the present day that it would appear to be somewhat of a strain to attempt to bring these two old forms in close proximity, when otherwise the series of forms in the ancient Phasmida is so complete.

I referred in my former memoir (p. 9) to the repetition, in the lower externomedian stem, of the features of the upper stem. If these two are looked upon as distinct externomedian and internomedian stems, we have an additional resemblance in this insect to some of the Protophasmida, though not to Breyeria; yet this repetition, "which appears to have no counterpart among living Ephemeridae," is in reality a feature constantly seen in paleozoic wings, and is indicative merely of simplicity and common origin such as we should naturally look for in early insects; and on this ground we may be justified in considering this insect as a representative of a distinct early type of Ephemerideous insects,—which may be called the Palephemeridae.

#### **Lithentomum Harttii.**

This insect I placed in a distinct family of Neuroptera proper, which from "having its nearest affinity to Sialina in modern times," I proposed to call Cronicosialina. Dr. Hagen also recognizes its Sialidan features and compares the wing to that of Chauliodes, adding "the paucity of the offshoots of the scapular branch is by no means exceptional . . . the living Chauliodes possesses only one."

Here again is an evident misapprehension of my language, for while the living Chauliodes has only one scapular branch, it has four or five offshoots of the scapular branch; a "branch" is not a main stem; and the course of the veins, as I have pointed out, forbids our supposing the ancient wing to have had more than one or two offshoots; only one is preserved.

A comparison of this wing with numerous paleozoic wings now convinces me that it should fall with many others in a group in which this branch may have several offshoots; at least it differs from them so little in general structure and in time that this disposition would seem to be the most rational one, and though Dr. Hagen seems to imply (though he does not explicitly state) that the character above mentioned was the only one laying claim to distinguish the Cronicosialina from the modern Sialina, I do not discuss this point here, as I shall soon do so to better advantage, in treating of the whole group.

**Homothetus fossilis.**

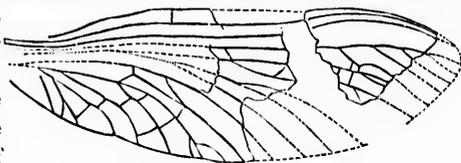
On account mainly of a transverse vein near the base of the wing, which I considered homologous with the areculus of modern Odonata, while almost every other feature of the wing was distinctively non-Odonate and generally Sialidan, I looked on this as the type of a distinct synthetic group, which I called Homothetidae, a family "forming the connecting link between the Neuroptera proper and Pseudoneuroptera."

Dr. Hagen, who has not seen the single original, says, "It is obvious that the wing belongs to the Sialina," and explains the so-called areculus as the end of a horny basal part of the wing, such as is seen in *Corydalis*. "The fragment," he says, "shows nothing foreign to the *Corydalis* type, excepting a smaller number of transversals."

The re-examination of this form after a special study of a considerable number of later paleozoic wings, some of which agree tolerably closely in general structure with *Homothetus*, apart from the supposed areculus in the latter, convinces me that I have been mistaken about this areculus. I find, indeed, that, when more closely scrutinized it just fails of reaching the scapular vein above, and that, what I strangely overlooked before, it is elevated, while the other veins about it are depressed; it lies, indeed, at a slightly higher level on the stone than the others, on a piece which shows a fracture farther away from the base of the wing, where the first separation of what I then considered the main scapular branch and the externomedian vein takes place. Upon this elevated piece that portion of the supposed branch lying between the so-called areculus and this separation is placed, and if we discard one we discard also the other; that is, these veins do not amalgamate at their base and curve downward (in passing baseward), but, as a closer examination shows, feebly and uncertainly it is true, both run parallel to each other and are separated by a slight interval, while the supposed obliquely curving basal amalgamation is something foreign to the wing, as, indeed, is shown by its also being elevated and not depressed.

Examined with this new light to seek for the basal attachments of the branching veins, a few faint indications, over that part of the fossil from which the wing has been flaked off (represented in the published drawing by dotted lines), show that there are, between what I formerly called the externomedian vein and the main scapular vein, two separate, parallel, longitudinal veins; moreover, that what I had looked upon as the basal part of the so-called externomedian vein is really only the edge of a flake of stone, beneath which, at a slightly lower point, this vein passes, the vein being unseen further toward the base than where the cross-vein strikes it.

If, then, within the basal fourth of the wing, between the stout scapular vein, and the so-called externomedian vein (which itself lies lower than indicated in the original drawing), there are two parallel, longitudinal veins, it is highly probable that the upper of them is directly connected with the vein which strikes the tip of the wing and carries several subequidistant, considerably oblique branches; and the lower with the vein or veins carrying the entire set of more longitudinal branches, between the preceding and what was formerly called the externomedian vein, somewhat in the manner I have indicated on



*Homothetus fossilis.* Corrected sketch.

the accompanying sketch correcting that formerly given, in which the lines marked in longer dashes give the conjectural course of the veins where they are not determinable, and the lines marked with shorter dashes the portions where faint indications on the stone render the determination somewhat more probable. This view is based on the complete change between the course of the nervules attached apically to the uppermost branching vein, and those below it, by which they are separated into two sets, intensified no doubt by the accident which has caused them to overlap where they are nearest together, but even in other respects very distinct.

On this basis we must make a very different interpretation of the entire venation. The scapular vein must be looked upon as a simple unbranched vein; the vein terminating at the tip, with the more oblique branches confined to the apical fourth of the wing, as the externomedian vein; the branches below this, as far as but not including what I formerly considered the externomedian vein, as branches of the internomedian vein; and the remainder of the nervules impinging on the lower margin, and more closely connected than the others by cross-veins, as branches of the anal vein.

Thus interpreted, the wing falls into a group of paleozoic insects which was perhaps the most numerous represented of all the old neuropterous types in carboniferous times, a group which is separated from all others by the complete independence of the medianal, and the lack of any inferior branches of the scapular vein,—a group to which the name of Homothetidae, with this complete alteration of the features by which it was at first characterized, may be applied.

As the lack of inferior branches to the scapular vein is an attribute at the present day of nearly all Pseudoneuropterous wings, and as it occurs in no true Neuroptera whatever, or certainly only in very exceptional instances, we find in Homothetus characters borrowed from prominent features of two great divisions of insects.

As stated above, Dr. Hagen suggested that the "areculus" could be explained by supposing it to indicate the point where, in the front wings of *Corydalis*, the horny basal part is separated from the membranous portion by a softer integument. This explanation would hardly be tenable on account of the distance in this case of the "areculus" from the base of the wing, but the facts given above show that the explanation is unnecessary.

#### ***Xenoneura antiquorum.***

A re-examination of both fragments of this wing in the light of Dr. Hagen's statements shows my figure to be correct in every point wherein it has been criticized, except in the wholly insignificant matter of omitting to give with sufficient distinctness what Dr. Hagen has compared to the "recurrent vein" of Hemersbidae. On the other hand, Dr. Hagen is incorrect in every statement of fact where his statement controverts mine. He has had the misfortune to publish his statements after an examination of only the more incomplete and less distinct of the two halves of the fossil. He complains that "the whole wing is shown by numerous parallel and very close longitudinal lines to have been placed beneath or above some part of a plant; on account of these lines some parts of the venation are less distinguishable." In the better St. John specimen these lines do not in the slightest degree interfere with the venation or its determination, but in at least two specific cases these lines on the Boston specimen have led Dr. Hagen into error.

One case is where he starts upon his theory that two partially overlapping wings are present, one of which I had overlooked,—a theory he could not possibly have maintained with the St. John specimen beside him. "Its hind margin," he says, "is a little below the hind margin of the main wing." Only a mere fragment of the hind margin exists in the Boston specimen, and therefore the marking on the stone which he interprets as the hind margin of a second wing is recognizable with little doubt, and a glance at its relations to the other lines proves at once that it is simply one of the "numerous parallel and very close longitudinal" lines which he refers to a plant. An examination of the reverse shows no such mark at all, and the glazed texture of the stone, peculiar to it where any part of the wing is found, does not extend, on either stone, beyond the limits of the wing as I have defined them.

Dr. Hagen would, however, probably base his double wing theory more upon his next point: that the branches of what I have called the externomedian vein (found on the outer detached fragment) are elevated, while the "corresponding sectors of the main wing" (by which I suppose he refers particularly to the scapular and internomedian veins of the parts on the basal piece) "are depressed." That is, that the detached fragment represents one wing, the basal piece another. But in the St. John specimen, and indeed, though less clearly, in the Boston specimen, we have absolute proof of the inaccuracy of this view, since the externomedian vein, whether on basal piece or detached fragment is, *throughout its course*, elevated or depressed, according to whether obverse or reverse is examined; the same is the case in the reverse sense with the internomedian vein, which is elevated, on both pieces, where the externomedian vein is depressed, and *vice versa*. A little more familiarity with paleozoic wings would have taught Dr. Hagen to expect this very feature.

Dr. Hagen is equally unfortunate with the scratch of a tool on the costal margin of the Boston specimen, which he would look for in vain on the reverse stone. If it had been shown on my former plate (fig. 5) it would have lain 3 mm. to the right of the outermost cross-vein figured; his making the other existing cross-veins "*therefore* very doubtful" is accordingly unwarranted. The upper branch of the mediastinal fork is exactly as I have figured it, and not as Dr. Hagen represents, as the St. John specimen shows more plainly than its Boston reverse. Dr. Hagen's "cellia" near this point are again the longitudinal lines of his plant. There is no sort of reason for claiming the "fork, as it is called by the author," of the scapular vein, as belonging to an overlying wing, since it does not exist.

Dr. Hagen says he is "not able to classify the insect, except that it belongs to the Neuroptera (*sensu strictiori*)," though he adds, "what we see of the venation is more nearly allied to the *Chauliodes* type than to any other." He further asserts that "the venation has no similarity to *Coniopteryx*, *Raphidia* and *Ephemera*, and bridges in no way the gulf between the Neuroptera and Pseudoneuroptera, as stated by the author." These are bare assertions, unaccompanied by any proof whatever, and it would therefore be waste time to consider them; it will be enough to say with regard to the first, that, if true, the wing cannot belong to the Neuroptera, as he himself claims it does. My own claim, supported by direct evidence which can be examined into, was that it formed a distinct and extinct family of Neuroptera. My later study of a larger series of paleozoic as well as of existing types confirms my first conclusion.

This new review of the Devonian insects alters somewhat the conclusions which we previously reached. *Gerephenera* is now considered a member of the group *Protophasmida*, formerly looked upon as its nearest ally, but from which it was regarded as distinct. The structure of *Homothetus* is shown to be different from what was formerly supposed, in taking from it its presumed Odonate affinities, but its position is otherwise retained, and the relation of the major part of the Devonian insects to later, carboniferous types, is shown to be more intimate than was supposed. This latter conclusion has been reached mainly by a study of forms discovered since the former paper was printed and which are yet unpublished; and it is the only point in which the thirteen several general conclusions formulated in my previous paper require any essential modification. It is even still true that notwithstanding the discovery of greater unity between the Devonian and carboniferous insects, the little fauna of St. John has features which instantly stamp it as distinct from the carboniferous; since, while most of its members belong to restricted groups which occur in carboniferous deposits, they are in most cases very different from the later members of these groups.

Instead, therefore, of the five species<sup>1</sup> being divided;—none to *Ephemeridae*, two to *Odonata*, and three to *Neuroptera* proper (and "probably" to *Sialina*), as claimed by Dr. Hagen, we find none whatever belonging to *Odonata*, but of the two so claimed, one referable to an ancient type of *Ephemeridae*, and one to an ancient type of *Phasmida*; while the remaining three belong to as many distinct families of ancient *Neuroptera*, doubtless related to, but still distinct from, *Sialina*, two of which were well represented in carboniferous times. The third, however, had, so far as yet discovered, no representative even among paleozoic insects, and has special interest from its distinct resemblance to the carboniferous *Protophasmida*,—a group afterwards differentiated as a special type of another order.

#### EXPLANATION OF THE PLATE.

I venture to add to this paper a plate engraved many years ago from imperfect and rude drawings of my own, which was discarded when I published my memoir on the Devonian insects, as insufficient and in part incorrect. It will serve, perhaps, to explain some of the changes my views have undergone, and to further illustrate to a slight degree some of the errors into which my critic has been drawn. All the figures excepting fig. 5 are of the natural size.

Fig. 1. *Homothetus fossilis*.

Figs. 2, 3. *Lithentomum Hartii*. These figures differ from those given in my formerly published plate to a considerable degree.

Fig. 4. *Dyseritus vetustus*.

Figs. 5, 6, 7. *Xenonura antiquorum*. Fig. 5 is made up from several camera sketches, and is enlarged about 20 diameters.

Figs. 8, 9. *Gerephenera simplex*. These represent both obverse and reverse, as they originally appeared. Fig. 9 is the one that has never been figured before. All or nearly all of these wings appear in reversed position on the plate. Fig. 9 should have been turned a little.

Figs. 10, 11. *Platphenera antiqua*. It will be noticed that fig. 11 shows what looks like a bit of the outer margin not far from the tip; this I suspect is simply a series of cross veins and was meant to represent only that; it is, however, given precisely in this way in my original drawing.

<sup>1</sup> Omitting *Dyseritus*, too imperfect for any satisfactory discussion.

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