1436

KANSAS PERMIAN INSECTS.

PART 16. THE ORDER PLECTOPTERA (Contd.): THE FAMILY DOTERIDAE, WITH A NOTE ON THE AFFINITIES OF THE ORDER PROTOHYMENOPTERA.

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ABSTRACT.

This part completes the author's work on the Lower Permian Mayflies in the Yale University Collection, by dealing with the problematical family Doteridae, containing only two species: *Doter minor* Sellards (type lost) and *Eudoter delicatulus* n.g. et sp. The author gives a restoration of the wing of *Eudoter* and concludes that the family were true Mayflies and belonged to the Permoplectoptera. As the genus *Asthenohymen* Till. (Order Protohymenoptera) was wrongly placed by F. M. Carpenter as a synonym of *Doter* Sell., the occasion is taken to correct the synonymy and also to discuss the true position of the Protohymenoptera and their relationships to the Megasecoptera and Hymenoptera.

Amongst the fossil insects originally collected and described by E. H. Sellards from the Lower Permian of Kansas, there was a single specimen of a small, delicate insect resembling a Mayfly, which Sellards named *Doter minor* (Sellards, p. 355, 1907). This specimen showed the abdomen, cerci and hindwings. The right hindwing is folded mid-longitudinally, so that the posterior half is turned forwards and lies upon the anterior half; the left wing is also folded, but obliquely from the base to a little beyond halfway along the posterior margin, so that more of the distal venation of this wing can be made out clearly. In his figures (Sellards, p. 354, Fig. 13, 1907) Sellards not only showed this specimen as it actually appeared on the rock, but he also attempted to restore the two hindwings completely.

Two very unfortunate occurrences have to be noted with regard to the genus *Doter*. The first is that Sellards' type is lost, together with a number of other types of his. The second is that Dr. F. M. Carpenter, assuming Sellards' figures to be inaccurate, advanced the opinion (Carpenter, p. 347, 1930) that my genus *Asthenohymen* (Tillyard, p. 117, 1924), belonging to the Order Protohymenoptera, was in reality only synonymous with *Doter* Sellards. Following an exchange of correspondence, however, Doctor Carpenter concluded (This Journal, vol. 24, p. 21, 1932) that he had mistaken a specimen of *Asthenohymen* in the Sellards collection for the type of *Doter minor* Sellards. He further added the *Asthenohymen* should

be restored as a valid genus and that *Doter* should be considered to be essentially as Sellards figured it.

It is, of course, a great misfortune that the type of such a rare and unique insect as this should have been lost. But there is, most fortunately, a specimen, No. 1014*a-b* in the Yale University Collection, which, though not belonging to the actual species *Doter minor* Sell., is at any rate closely allied to it. I propose to compare this specimen with Sellards' original drawings and description of *Doter minor*, which are all that we now have left to go upon in studying this species.

First of all, it is necessary to remark that I have found Sellards' drawings generally reliable. As far as I know, he has nowhere made any major errors in drawing, beyond those that are inseparable, as all students of fossil insect wings know, from the effort to follow out carefully the very faint impressions found in some fossil wings. Hence I shall assume that Sellards' upper figure in his Fig. 13, p. 354, of his 1907 paper is approximately correct and shows the venation of the two hind wings of *Doter minor* just as they appeared to him when viewed under the microscope. In the lower figures, in which Sellards has attempted to restore the complete venations of both wings, there is admittedly room for error to creep in. Such a restoration is admittedly a difficult matter, even for an expert, owing to the extreme faintness of the crossed impressions of the veins, and the possibility that the folding may have taken place actually along the line of one of the main veins of the wing, or even that a vein in the folded part may partly or wholly coincide with a vein in the unfolded part.

With this hypothesis as a basis for our study, we may now set down the characters in the venation of the genus *Doter* which are known for certain. These are as follows:

(1) The subcosta, Sc, runs not far from the costal margin to end up on the costa at a point less than one-sixth of the wing length from the apex.

(2) The radius, R_1, is a strong vein running below Sc and well separated from it except basally; it diverges slightly from Sc distally and ends on the costa slightly before the apex of the wing.

(3) The radial sector, Rs, is apparently four-branched; this vein, however, is interpreted by Sellards as radial sector plus media, the radial sector being, in his opinion, three-branched, the media simple.

(4) The anterior median (first cubitus, according to Sellards) is three-branched.

The veins restored by Sellards are three in number, viz., a five-branched vein which Sellards considers the second cubitus, and two simple veins which he considers anals. I should myself consider that the first of these veins is the posterior median, but I think it very unlikely that it was five-branched. The so-called anals of Sellards may well be the two cubitals, in which case the true anal veins were probably a set of very short veins lying close to the base of the wing posteriorly and very poorly chitinized, as is the case with the anal veins in the families Protereismatidae and Misthodotidae.

Sellards' figures show a few faint and irregular cross-veins. It is probable that there were more present than are shown, but that they were very faintly impressed on the rock.

The new specimen resembles *Doter minor* very closely in size, general shape of body and wings, and in the remarkable condition of the wings, which are spread out much as in Sellards' specimen and also folded longitudinally much in the same way. We know that, generally speaking, only wings with a very weak membrane become fossilized with longitudinal folding. It is clear that, in the case of both *Doter* and the new fossil, the membrane must have been very weak and also the veins very lightly chitinized.

The new specimen is more complete than the original type of *Doter minor* Sell. in that it has the head, thorax and abdomen complete, together with the left foreleg (nearly complete), portions of the left middle and hind legs, the left forewing and both hindwings. All three wings are folded longitudinally, much in the manner of Sellards' specimens. The abdomen shows clearly ten distinct segments, with large pale spiracular areas on segments 1-8, and ends in three elongated, multi-articulate tail-filaments. In *Doter minor*, only the two cerci were present.

As regards measurements, Sellards gives the length of the abdomen of *Doter minor* as 4 mm., exclusive of the cerci, and that of the hindwing as 7 mm. In the new fossil, the length of the whole body is approximately 7.6 mm., of which the abdomen accounts for slightly over 4 mm., while the measurements of the wings are, forewing and hindwing alike, approximately 6 mm. In the reverse specimen, I have succeeded in uncovering all three tail-filaments for a distance of nearly 5 mm.; at this point, they are still apparently "going strong," and we may assume that they were most probably very much longer than the body of the insect.

I think there can be no doubt that both *Doter minor* and the new fossil belong to the Ephemeroid complex of forms. Sellards says of his species (l.c., p. 355):

"The genus clearly cannot be referred the Protereismephemeridae, the venation being altogether different. It is possible that the genus will be found to fall within the Protephemeridae."

The first point to be determined is whether the new fossil belongs to *Doter minor* or not. The only striking difference, apart from the venation, is the presence of three caudal filaments instead of two. It might be argued that this was only a sexual difference, as examples are known in recent Mayflies in which the male of a species possesses only two caudal filaments while the female possesses three. The new fossil is, however, most probably a male. What the sex of Sellards' specimen was is not at all clear, but the absence of any sign of external genitalia suggests that it was a female. In any case, we must decide against the two specimens belonging to the same species, or even to the same genus, because, as we shall see in the sequel, the working out of the venational scheme for the new fossil gives a result which differs considerably from that of *Doter minor*, even if we allow for all possible reasonable errors on Sellards' part.

Turning then to the reconstruction of the venation in the new fossil, we note first of all that we have five wing impressions to study, viz., the single impression (obverse) of the left forewing, and both obverse and reverse impressions of right and left hindwings. All five impressions offer something of value, and all have been carefully studied by me. But the one which lends itself most readily to reconstruction is the right hindwing. The main reason for this is that this wing happens to be folded longitudinally parallel with its long axis, so that the overfolded veins all run across the membrane at very marked angles to the veins in position, thus assisting the difficult task of restoring them accurately.

Taking the unfolded portion of the wing first we note that Sl and R_1 are of the usual Mayfly type, and closely resemble those veins as shown by Sellards for *Doter minor*. There is, at first sight, as Sellards states for *Doter*, no sign of a costal brace; but it is highly probable that a very small one may have been present at the extreme base of the wing, as there is a faint indication of this in the left hindwing of the new fossil. Very faint cross-veins can be just made out in the costal and

subcostal spaces, and these are irregularly placed and at right-angles to the main veins, as in true Mayflies. Rs arises from R at about one-sixth of the wing length, and appears at first sight to be a five-branched vein, the branches being arranged in two negative triads, as follows:

$$R_2\ (-),\ IR_2\ (+),\ R_3\ (-),\ IR_3\ (+) \text{ and } R_{4+5}\ (-).$$

However, if we follow R_3 distally, we shall see that it also has a triad on it; for R_{3b} can be seen descending to the longitudinal fold, while R_{3a} runs to the apex just above the end of the fold.

In order to complete our picture of Rs, we must now attempt to follow those branches which are bent at the fold. There is a very short IR_{3a} close to the end of the fold, and this is followed by the bent distal ends of R_{3b}, IR_{3b} and R_{4+5} in turn, the last-named having been bent at the fold at about half its length from the primary fork of Rs.

Returning to our examination of the basal, unfolded portion of the wing, we can now pick up, somewhat faintly, the vein MA running just below Rs and diverging from it at a slight angle. An examination of its origin, in both fore and hind wings, shows that it either arises with Rs or just touches it close to its origin; the vein itself is not clearly enough impressed for us to make certain which is the case. But it will be seen that, on either interpretation, the condition is similar to that found in the Protereismatidae. MA can be followed straight to the margin of the fold, where it is turned back obliquely and develops a fairly large triad.

The courses of the main veins posterior to MA are not at all clear in any of the wings. We therefore return to an examination of the extreme base of the wing in an attempt to follow them out. Here we note at once an arched formation of a thickened basal vein, very similar to that which I have termed the third axillary in *Protereisma,* from which the anal veins are developed. Only, in our new fossil, it is impossible to make out more than the slightest traces of two or three descending veins from this structure. Distally, however, where it turns up to meet the main stem of Rs + MA, three main veins appear to come off from it. Of these the most anterior appears to descend from Rs + MA, and is clearly MP. In one wing it appears to fork just before reaching the fold, in another sooner, but the impression is not at all clear. As our examination of the veins on the folded por-

tion of the wing distally shows a group of three diverging slightly from one another as if forming a triad, I have allotted these to MP, which will then have a triad arising more basally than that of MA, just as in *Protereisma*. The other two veins which arise from the end of 3Ax, below its transverse connecting piece with Rs + MA, are obviously the two cubitals, CuA and CuP. The distal portion of CuA can be followed across the fold; but, owing to the fact that the fold is torn away basally from this point, it is impossible to follow the courses of these veins any further. There is, however, so wide a space to be filled between these two veins, in any reconstruction in which the posterior margin is continued back to the base in a steady curve, that I consider it logical to restore the vein CuA with descending branches, though it is impossible to say whether they formed a true triad or not.

In the restoration of the wing shown in Fig. 3, the uncertain parts are dotted, as are also all the cross-veins. Making all due allowance for the formation of these doubtful veins, it will still be seen that this new fossil possesses all the main venational features of a true Permian Mayfly, and as such, therefore, I propose to classify it.

It is possible now to suggest an explanation of Sellards' drawing of the wing of *Doter* which will bring it more closely into line with that of the new fossil. Sellards may have missed a short, faint interpolated branch between R_2 and R_3; the addition of this would bring the formation of Rs into line with that of the new fossil, except for the absence of the terminal triad on R_3. MA has a single triad, as in the new fossil, and it is possible that the branching of MP may be somewhat variable, or that MP_2, which I have considered to be a simple vein in the new fossil, may be in reality branched.

It would then appear that the two forms, *Doter* and the new fossil, are sufficiently alike to be included in a single family, Doteridae, belonging to the Suborder PERMOPLECTOPTERA Tillyard, on account of their fore and hindwings being alike, and making the third family of that Suborder so far discovered.

Family DOTERIDAE.

Small, delicately formed Mayflies with slender bodies, long tail-filaments and delicate wings with weak membrane. Venation as far as known generally similar to that of the other families of the Suborder; costal brace-vein small and weakly

formed, or absent; cross-veins few, irregularly scattered and extremely weak.

Only two genera are known, which may be distinguished as follows: -

Tail-filaments two only; R_3 a simple vein, without a triad. Genus *Doter* Sell.

Tail-filaments three; R_3 with a well developed triad. Genus *Eudoter* n.g.

Genus DOTER Sellards.

(Fig. 1.)

Doter Sellards, This Journal (4), 23, p. 355 and Fig. 13, p. 354, 1907.
Doter Handlirsch, *Densk. Akad. Wiss. Wien. Math. Nat. Kl.*, 82, p. 22, 1919.
NEC *Doter* Carpenter, *Psyche*, 37, pp. 356 *et seq.*, 1930.
NEC *Asthenohymen* Tillyard, This Journal (5), 8, p. 117, 1924; 5, 11, p. 63, 1926.

Sellards originally described both genus and species together, so that it is impossible to say which characters he regarded as generic. The following amended definition of the genus is now given:

Abdomen slender, subcylindrical, ending in two long, slender, multi-articulate caudal filaments (cerci). *Wings* delicate, with weak membrane, rather weak main veins and

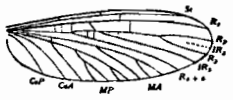

Fig. 1. *Doter minor* Sell. Left hindwing, drawn with apex to right, showing Sellards' interpretation of the courses of the veins, but with the modern notation for the Plectoptera attached. The dotted vein, IR_2, is not shown in Sellards' figure, but it is suggested here that it was overlooked by him.

almost evanescent cross-veins; in shape, elongate oval, about three times as long as broad. Costal brace-vein apparently absent. Sc and R_1 simple, subparallel, extending nearly to apex of wing. Rs apparently four-branched, the branches being R_{2a}, R_{2b}, R_3 and R_{4+5}. (It is suggested that Sellards may have missed the middle member of a triad, and that Rs in this genus is really five-branched, the branches then being R_2, IR_2, R_3, IR_3 and R_{4+5}.) MA with a triad, MP apparently five-branched. CuA and CuP simple veins. Anal veins not visible, evidently very short.

Genotype:—*Doter minor* Sellards.

Fig. 2. *Eudoter delicatulus* n.g. et sp. Specimen No. 1014*a*. Holotype, obverse. Forewing 6 mm. long.

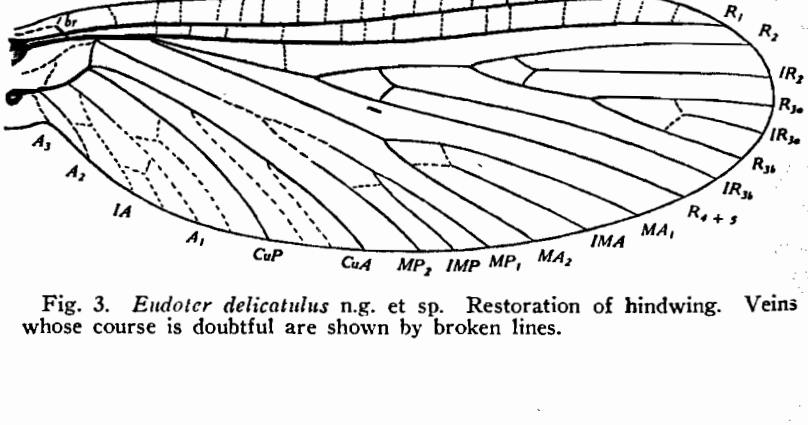

Fig. 3. *Eudoter delicatulus* n.g. et sp. Restoration of hindwing. Veins whose course is doubtful are shown by broken lines.

Doter minor Sellards.

(Fig. 1.)

Nec *Doter minor* Carpenter, *Psyche*, 37, pp. 356 *et seq.*, 1930, and This Journal (5), 22, pp. 126-129 and Figs. 7, 8, 1931.

The type specimen, lost since 1927, showed the abdomen and metathorax, trending posteriorly to the left, with the two hindwings outstretched almost at right angles to the body. The right wing is folded longitudinally from end to end, a large number of main veins crossing the fold obliquely. The left hindwing is folded obliquely so that a little more than the basal half of the posterior margin is turned well over so as to lie as far forward as Rs; this fold extends as far as the end of MP. The cerci extend closely parallel to one another from the end of the abdomen, but are broken off distally.

Length of abdomen 4 mm., of *cerci* (estimated length of preserved portions) 2.5 mm.; *hindwing*, length 7 mm., *breadth* (estimated) 2.5 mm.

Fig. 1 shows Sellards' restoration of the hindwing, enlarged, with the addition of the suggested vein IR_2 (broken line). The notation is the modern notation for Plectoptera.

Type originally in Sellards' Collection at Austin, Texas, but apparently (*teste* F. M. Carpenter, 1931, *in litt.* and *teste* C. O. Dunbar, *in litt.*), thrown out accidentally by the janitor of the Geology Department at the University of Texas, and lost.

Genus Eudoter n.g.

(Figs. 2-4.)

Greek εὐ well, δωτὴρ giver. One must acquit Sellards of any form of humour in dubbing his little insect *Doter*; but the name was certainly prophetic, for its interpretation has given more trouble than that of almost any other Kansas fossil. The new genus, which I have named *Eudoter*, "a cheerful giver," is certainly more pleasant to handle, though not easy to study.

General facies and size much as in *Doter*, but distinguished by the possession of three tail-filaments and by a complete series of triads on Rs, viz. R_2, IR_2, R_{3a}, IR_{3a}, R_{3b}, IR_{3b} and R_{4+5}, the intercalated members being convex; these triads are arranged exactly as in the families Protereismatidae and Misthodotidae.

Genotype:—*Eudoter delicatulus* n.sp.

Horizon:—Lower Permian of Kansas.

EUDOTER DELICATULUS n.sp.

(Figs. 2-4.)

♂ Imago:—

Total length of body 7.6 mm., of *abdomen* 4.2 mm., of *tail-filaments* broken) 4.7 mm. *Hindwing,* length 6 mm., *breadth* (estimated) 2 mm.

The veins being very weak, it is difficult to determine which of the two impressions is the obverse. The left hindwing in Specimen No. 1014*a* definitely shows Sc as a concave vein, and is therefore selected as the obverse impression.

Specimen No. 1014*a* shows the whole insect with the exception of the right forewing and most of the legs and antennae. The abdomen is broken at seg. 2, and the posterior portion is bent at an angle of about 135° to the line of the head and thorax, with the three caudal filaments stretched out together straight in line behind it, to the right. The bases of the two left wings slightly overlap the thorax, which is crushed somewhat sideways; the right hindwing shows the axillaries attached to the metanotum. Specimen 1014*b* (reverse) is somewhat less complete, the forewings being entirely missing and the tip of the left hindwing broken off. In both specimens the head is crushed down sideways partly into the prothorax.

Head (crushed sideways) approximately 0.8 mm. long by 1.0 mm. wide, with the compound eyes small, rounded, placed laterally. A small portion of one antenna visible; it was evidently a short, subulicorn organ consisting of few slender cylindrical segments.

Thorax: *Prothorax* (crushed) apparently short, narrower than head. *Mesothorax* large, considerably humped, 1.7 mm. wide as impressed on the rock, the spiracles apparently large and well defined. *Metathorax* somewhat smaller than mesothorax but well developed, the spiracles smaller but quite conspicuous. *Legs*:—Most of the left foreleg is preserved, consisting of the femur, fairly stout, short, 0.7 mm., broken in the middle and bent back upon itself, followed by the tibia, slender, cylindrical, 0.7 mm. long, and the first segment of the tarsus, 0.5 mm. long, slightly narrower than the tibia; slightly beyond, after a break, can be seen remnants of two short distal segments, either the fourth and fifth, or else the fifth and part of the claws. A short basal portion of the left hind leg is also preserved, showing the coxa, trochanter and basal half of the femur.

Wings (Fig. 3) :—In the obverse specimen, the left forewing is complete, but is folded longitudinally and also somewhat crumpled basally, so that the venation is very difficult to make out. The fold runs from the third axillary in a straight line to a point well below the apex, about where R_{4+5} ends, but the distal portion of the actual fold is irregularly broken. The left hindwing is broken off distally at about two-thirds of its length and is also longitudinally folded and slightly crumpled. The right hindwing is the best preserved, lying attached to the metathorax without any overlapping, the axillaries clearly visible and practically the whole wing preserved. This wing is folded longitudinally, parallel to the costal margin of the wing, in such a way that the folded portion at its greatest width just overlaps the subcosta; a small break in the rock has torn away a portion of the basal half of the fold in the obverse, but this part is complete in the reverse specimen. In this wing, the structure of Sc, R_1 and Rs can be completely made out, and the passage of the other main veins across the folded area is clearer than in the other two wings; hence it has been mainly used in the reconstruction shown in Fig. 3. As the details of the venation have been already given in the description of the reconstruction, it is only necessary to add here that no attempt has been made to map accurately the cross-veins, which are excessively delicate but appear to be fairly numerous; only those which can apparently be made out under oblique light in the costal and subcostal areas have been shown in Fig. 3, and some of these might easily be mere scratches on the rock.

Careful search was made for the costal brace-vein, with the result that a remnant of it was discovered at the base of the left hindwing in the reverse impression (Fig. 3, *br*). It appears to be of the type found in the Misthodotidae, but smaller and more weakly formed.

Abdomen (Fig. 4) with ten distinct segments, each showing a chitinized and slightly darkened tergal and sternal portion separated by a pale, membranous pleural area in which the spiracles can be seen in segs. 1-8. The abdomen is impressed on the rock with the last eight segments torn away from the first two and bent at an obtuse angle to them, but the boundaries of the segments are all fairly clearly marked. On seg. 9 there can be seen a hardened chitinous structure of a dark colour, which appears to arise from a semi-circular area situated partly on seg. 8 and projects onto seg. 10; the sternite of

seg. 9 also appears to be excised triangularly. As no structure similar to this is known in the females of Mayflies, I interpret this provisionally as the more or less crushed male genitalia, though the parts themselves cannot be clearly made out. It is possible that the forceps may have been turned over so as to point forwards instead of backwards.

Segs. 2-7 show clearly the presence of strong transverse carinae strengthening the tergites. These are not shown in the outline in Fig. 4.

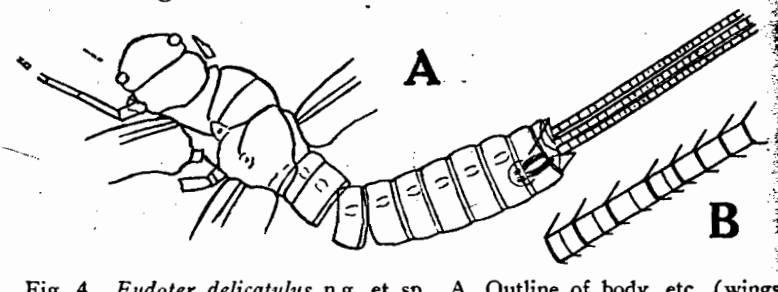

Fig. 4. *Eudoter delicatulus* n.g. et sp. A, Outline of body, etc. (wings mostly omitted); length of specimen 7, 6 mm. B, Portion of right cercus, showing segments, subsegments and setae (× 37).

The tail-filaments are well preserved for a distance of nearly 5 mm. from the end of the abdomen in the reverse impression, but only for about 3 mm. in the obverse. The *cerci* (Fig. 4B) are multi-articulate and obviously extended far beyond the limits preserved in the fossil; each segment was cylindrical, longer than wide, and was furnished at its outer posterior end with a strong bristle. Many of the segments are partially divided into two subsegments by a fine chitinous ring (Fig. 4B); on the inner side, there appear to have been shorter and finer hairs both at the ends of the segments and subsegments. The *appendix dorsalis* resembles the cerci, but the hairs appear to have been short and weak, as on the inner side of the cerci. The form and strength of the tail-filaments show that the specimen was an imago, although the wings are slightly tinted.

Types:—*Holotype obverse*, Specimen No. 1014*a*, and reverse, No. 1014*b*, in Yale University Collection.

This paper concludes the study of the Lower Permian Mayflies in the Yale University Collection of Kansas fossil insects. The long gap between the publication of Parts 15 and 16 is entirely due to my long and serious illness during most of 1933 and 1934. It has only recently been possible for me to

take up this work again, but I hope to conclude this series of studies before very long.

A NOTE ON THE AFFINITIES OF THE ORDER PROTOHYMENOPTERA.

In his two papers on the Protohymenoptera, Dr. F. M. Carpenter (1930, 1931) has advanced the theory (following Martynov, 1930) that the Protohymenoptera are merely specialized members of the Order Megasecoptera, and have nothing to do with the Hymenoptera proper. He also questions the interpretations of the wing-venation which Martynov and I gave for this Order, and suggests (p. 348, Pl. 15, Fig. 1, 1930) a new interpretation based on better material than that which Martynov and I had for studying.

Taking the venation first, it is obvious that the determination of the obverse and reverse impressions is a difficult matter, unless the specimens are in very good condition. For the wings are flat and glassy; and it is not easy to say, in a poor specimen, whether the radius, for instance, is convex or concave. Originally I made my determinations on the distal end of R, where there is a short vein which I considered to be Rs. If, as Carpenter avers, this vein is really a part of R_1, then it is clear that my determinations of obverse and reverse specimens must be changed, since Rs is a concave vein and R_1 a convex one.

There are no longer in my possession any specimens of Protohymenoptera, except a very poor one which I found myself at Elmo in 1928. But, with the discovery of further genera by Martynov in Russia, and with the addition of much better material from Kansas, it seems clear that Carpenter has established his case for a re-interpretation of the venational scheme. The fact that this scheme, so apparently simple on the face of it, has now to be considered very complex and as forming the end-term of a phyletic series of high specialization, does not seem to me to weigh against his interpretation, but, on the contrary, commends it. For it is now possible to understand how this remarkable type of venation came into existence. I propose here to accept Carpenter's venational scheme for the Order Protohymenoptera, and also to apply it to the Order Hymenoptera, thus bringing the venational notations of the two Orders once more into line. In order to make the position clear, I give herewith a Table showing the various

interpretations of the venational schemes of the two Orders, by myself originally (1924), by Martynov (1930) and by Carpenter (1930), together with the new scheme as applied to the Hymenoptera.

TABLE OF THE VENATION OF THE FOREWING IN THE ORDERS PROTOHYMENOPTERA AND HYMENOPTERA, AS INTERPRETED BY TILLYARD (1924), MARTYNOV (1930) AND CARPENTER (1930).

	Order Protohymenoptera.			Order Hymenoptera.	
Vein.	Tillyard 1924	Martynov 1930	Carpenter 1930 (accepted by Tillyard, 1936)	Tillyard 1924	Tillyard 1936 (new notation)
1	Sc	Sc	Sc	Sc	Sc
2	R_1	R_1	R_1 (part)	R_1	R_{1a}
3	Rs	R_2	R_1 (part)	Rs	R_{1b}
4	M_1	R_3	R_{2+3}	M_1	R_{2+3}
5	M_2	R_4	R_{4+5}	M_2	R_{4+5}
6	M_{3+4}	R_5	MA	R_{3+4}	MA
7	Cu_1	MA	MP	Cu_1	MP
8	Cu_2	MP	Cu_1	Cu_2	Cu_1
9	1A	Cu	Cu_2	1A	Cu_2
10	2A	A	1A	2A	1A

Reference Figures:

Order Protohymenoptera:
Tillyard, 1924, p. 113, Fig. 1, *Protohymen permianus* Till.
Martynov, 1930, p. 81, Fig. 4, *Aspidohymen extensus* Mart.
Carpenter, 1930, p. 348, Pl. 15, Fig. 1, *Protohymen permianus* Till.
Order Hymenoptera:
Tillyard, 1924, p. 119, Fig. 4, *Macroxyela* sp.; p. 120, Fig. 5, *Sirex* sp.

It should be noted that both Tillyard in 1924 and Martynov in 1930 must have inadvertently mixed up the obverse and reverse impressions of the fossil wings of Protohymenoptera.

It should also be noted that, now that Carpenter's amended notation is accepted, there are four Orders known in which there is only a single convex anal vein, 1A, viz. Odonata, Megasecoptera, Protohymenoptera and Hymenoptera.

Regarding Martynov's arguments (pp. 77-80, 1930), we may shortly recapitulate them as follows:

(1) The wings of the Protohymenoptera closely resemble those of the Megasecoptera and should be regarded as a specialized offshoot from them.

(2) Therefore the Protohymenoptera belong to Martynov's subdivision Palaeoptera of the Subclass Pterygota, and must have rested with their wings outspread.

(3) The Hymenopterous type of venation, on the other hand, in Martynov's opinion, is related to that of the Megaloptera and Mecoptera.

(4) Therefore the Hymenoptera are Neoptera and have nothing to do with the Protohymenoptera, which are Palaeoptera.

(5) The name Protohymenoptera is (p. 83) "somewhat pretentious," and Martynov proposes to change it to "Synsecoptera."

We can deal at once with (4) by stating that the name Protohymenoptera will continue to have priority, in spite of Martynov's objection to it as a "somewhat pretentious" name. The word "pretentious" would imply that I was using a name in order to attach a significance to the group which I myself did not really believe in. I do not think that Martynov really intended to convey this meaning, but only that, in his opinion, the word conveyed too close an indication of an affinity in which he does not himself believe.

Carpenter, in any case, continues to use the name Protohymenoptera, and I think that, even if the Protohymenoptera be sunk to the rank of a suborder of the Megasecoptera, this name must stand, and that the name Synsecoptera can only be regarded as a synonym of it.

As regards the Palaeopterous affinities of the Protohymenoptera, they are clear enough. But a difficulty arises in that the family Asthenohymenidae contains no single specimen with wings outspread, but includes several with the wings folded. In my opinion, the wings in these specimens appeared to be folded roofwise, although the abdomen was not preserved. Martynov, however, would explain this as follows (p. 78) :— "It is true that among Asthenohymenidae specimens 'occur in which one wing is laid over the other,' but the same takes place in the Zygoptera, and this manner of resting in the Zygoptera in no way proves that they are allied to Hymenoptera or to any other Holometabola or, even, to Neoptera." This argument is, of course, unsound; for it is well known that the wings of Zygoptera are folded exactly as are those of the Mayflies, except for the great obliquity of the thorax and the change in position of the wing-sheaths of fore and hindwings in the larva. In consequence of this, the wings of Zygoptera are directed more or less backwards, instead of upwards as in Mayflies, and also the hindwings lie outside the fore, instead of inside them, in the position of rest, as in

Mayflies. Therefore, when it is seen that specimens of *Asthenohymen* rest with their wings folded, it should be realized that the chances are much greater that this folding is similar to the folding which occurs in the great majority of other winged insects, rather than to that which occurs in the Zygoptera *and nowhere else.*

However, the problem is solved, once and for all, by the discovery, in the Harvard Collection of Kansas Permian insects, of a practically complete specimen of *Asthenohymen* in which all four wings are folded back over the abdomen in a rather flattish, roofwise manner. This is Specimen No. 3059*ab* in the Museum of Comparative Zoölogy at Harvard, figured by Carpenter (Fig. 7, p. 126, and Fig. 8, p. 128, 1931) as *Doter minor* Sell. Its correct name is, of course, *Asthenohymen dunbari* Till.

I must now ask Martynov the following question:

> In view of the fact that the genus *Asthenohymen* undoubtedly rested with its wings folded roofwise over its abdomen, what reasons can you give for classifying it as a Palaeopteron, seeing that you have defined that subdivision of the Pterygota as those insects which are incapable of folding their wings back in a roof-like manner?

This is, indeed, a poser! It must now be evident that a group of insects, the Order Megasecoptera, which began as Palaeoptera, have, within the limits of a single small derived group, the Protohymenoptera, evolved into a highly specialized Neopterous type, the family Asthenohymenidae! I do not suppose that anybody will attempt to claim that *Asthenohymen* should be separated from its obvious relatives *Protohymen* and *Permohymen,* which rested with their wings outspread, in order to preserve the two subdivisions Palaeoptera and Neoptera, which are now seen to cut across the actual phylogenies of these ancient groups. The only logical course is to suppress the two groups Palaeoptera and Neoptera, and adopt a classification more in keeping with the facts.

Surely it must have been obvious for a long time that all Neoptera have been derived from extinct Palaeopterous types. Now the fossil record shows us a group, Protohymenoptera, of either ordinal or subordinal rank, whichever you prefer, in

which the change is seen actually taking place. Two genera, *Protohymen* and *Permohymen*, are undoubtedly Palaeopterous, and the third, *Asthenohymen*, is just as undoubtedly Neopterous!

As regards the venation of the Protohymenoptera, I have already indicated that I accept Carpenter's modifications of my original notation. There is, to my mind, no reason why these modifications should not be also applied to the venational scheme of the Order Hymenoptera.

We have now to consider the question of the ovipositor. Carpenter (p. 371, 1930) pointed out that it would hardly be expected that the ancestors of the Hymenoptera would have had such well developed cerci as he found in complete specimens of *Asthenohymen*. But he failed entirely to note that *the ancestors of the Hymenoptera must have had a complete external ovipositor*, seeing that the Hymenoptera are *the only group of Holometabolous insects in which such an organ is developed*. And yet he states that this discovery of his "is the first unquestioned instance of such a structure in a palaeozoic insect"! Then, one may well ask, how does the presence of this large and complete ovipositor strengthen the argument that Protohymenoptera are only specialized Megasecoptera, seeing that, out of all the complete Megasecoptera already known, there is not a single one in which an ovipositor is present?

It is admitted that complete ovipositors occurred in many of the Protorthoptera (although not, so far, recorded). But they did not occur in any known Palaeodictyoptera, Megasecoptera, or Plectoptera. How then can *Asthenohymen*, possessing a complete archaic ovipositor, be descended from any one of these Palaeopterous groups?

To my mind, the discovery of the external ovipositor in *Asthenohymen* greatly strengthens my original argument that the Protohymenoptera are the ancestors of the Hymenoptera.

Let us now recapitulate the argument for this:

(1) The general plan of the venation in Hymenoptera can be interpreted logically in terms of the venation of Protohymenoptera. Attempts to interpret it in terms of the venation of any other known Order have not so far been successful.

(2) The wing-membrane of the Hymenoptera is hard and glassy, as in the Protohymenoptera (and, incidentally, the Odonata).

(3) The venational scheme of the Hymenoptera shows very strong main veins connected by strongly chitinized cross-veins which divide the wing into a rather small number of large cells. The same type of venation occurs in the Protohymenoptera, and, adopting Carpenter's new notation, the venation of the Hymenoptera can be logically derived from that of the Protohymenoptera. (Incidentally, again, the only other Order in which a similar type of venation occurs, but with a considerable increase in the number of cells, is the Odonata.)

(4) The structure of the head, antennae and eyes in *Asthenohymen* are such that it could easily be the ancestor of the Hymenoptera. It is true that the ocelli have not been seen; but it would require a very well preserved specimen indeed to show these organs.

(5) The legs in *Asthenohymen* have only a three-segmented tarsus. The tarsi in Hymenoptera are five-segmented. Therefore the genus *Asthenohymen* cannot itself have been the ancestor of the Order Hymenoptera. But Carpenter has insisted that the tarsi of Megasecoptera were all five-segmented, in spite of Handlirsch's figures showing them as four-segmented. Legs of *Protohymen* and *Permohymen* have not yet been found. But it seems reasonable to suppose that *Asthenohymen*, which is by far the most advanced member of the Order in other respects, is also ahead of these more archaic genera in the structure of its tarsi, and that, therefore, the Order Protohymenoptera, like the Coleoptera, may have included forms with five-segmented tarsi as well as forms with three-segmented tarsi.

(6) The abdomen of *Asthenohymen* apparently possessed eleven segments and a pair of elongated cerci. There is nothing in this which precludes the Protohymenoptera from being considered as ancestors of the Hymenoptera, which, like all other winged insects, must have been descended from older types having the abdomen and cerci of this form.

(7) The ovipositor of *Asthenohymen* is of the complete, archaic type. It is the same in Hymenoptera alone of all the Holometabolous Orders. An ovipositor does not occur in the Megasecoptera. Therefore the genus *Asthenohymen*, at any rate, cannot be descended from any known form of Megasecoptera, and the Order Protohymenoptera should retain full ordinal rank and not be merged as a suborder of the Megasecoptera.

My conclusion is that the Order Protohymenoptera shows affinity with both Megasecoptera and Hymenoptera. It should be regarded as a specialized offshoot from the common ancestor of Megasecoptera and the Odonatoid complex (such ancestor must have possessed an ovipositor, since it occurs in all

Zygoptera and some Anisoptera), and, at the same time, as a remnant of the group from which the Hymenoptera have been evolved.

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