THE LOWER PERMIAN INSECTS OF KANSAS. PART 4. THE ORDER HEMIPTERA, AND ADDITIONS TO THE PALEODICTYOPTERA AND PROTOHYMENOPTERA.

F. M. CARPENTER*

Our knowledge of the geological history of the Hemiptera has been greatly advanced in recent years by the discovery of a large series of Homoptera in the late Permian Rocks of Russia and Australia. Only a few species of the order have been found in the Lower Permian of Kansas, but their greater age gives them special significance. In the Yale collection from this formation Tillyard obtained four tegmina of Homoptera, each of which he considered a distinct species (1926). In Dr. Sellards' collection, which has been loaned to me for study, I find one good tegmen, and in the Harvard collection, sixteen specimens, one of which shows many details of the body.

The existing Homoptera are usually grouped into two divisions: Auchenorrhyncha and Sternorrhyncha.[1a] The former has the more primitive wing venation, inasmuch as the anal area (or clavus) of the Sternorrhyncha is reduced and the second anal vein is absent. The body structure of the Auchenorrhyncha is also generally considered to be more primitive than that of the Sternorrhyncha, except for the antennae. In the Auchenorrhyncha the antennae are reduced to two short segments, terminating in a bristle or style; in the Sternorrhyncha they consist of at least three segments and may include as many as twenty-five. Now all the Homoptera of the Kansan Permian are so closely related that they can be placed within a single family, but I do not believe that this family can be assigned to either the Sternorrhyncha or Auchenorrhyncha. Tillyard placed one of the Lower Permian species, *Permopsylla americana* Till., within the Sternorrhyncha, because the single type specimen apparently lacked the clavus of the tegmen. In the Harvard collection there are ten specimens of Permopsylla and all of them possess a large clavus containing two anal veins.

* National Research Fellow. These studies have also been aided by grant No. 280 of the Bache Fund, National Academy of Sciences, and a Sheldon Traveling Fellowship from Harvard University.

[1a] Myers and China have recently established a third division (Coleorrhyncha) for the family Peloridiidae (Ann. Mag. Nat. Hist. (10) 3, 282-293).

AM. JOUR. SC.—FIFTH SERIES, VOL. XXII, No. 128, AUGUST, 1931.
8

This fact, of course, signifies that the absence of the anal area in the type specimen is merely due to lack of preservation and such a conclusion is supported by the condition of the fossil itself, for the second cubitus and even part of the first cubitus are missing, as indicated by Tillyard in his drawing of the wing (Fig. 7, p. 392). The venation of the tegmen of *Permopsylla americana* is therefore identical in important features with that of the three other Lower Permian species, *Archescytina permiana, Permoscytina kansasensis,* and *P. muiri,* which Tillyard placed in the Auchenorrhyncha. So far as their wing venation is concerned, these insects might belong to the division Auchenorrhyncha, as he supposed, and this, of course, was all that he had on which to base his conclusions. But one of the Harvard specimens of Archescytina shows part of the body, including the antennae, *which are very long and consist of at least twenty-five segments.* This type of antenna is absolutely foreign to the Auchenorrhyncha, in which the antennae, as I have mentioned above, are always two-segmented. It appears, therefore, that these Lower Permian Homoptera were characterized by a combination of the primitive antennae of the Sternorrhyncha and the primitive tegmina of the Auchenorrhyncha. We would hardly be justified in placing these Permian species within the Sternorrhyncha, considering the well-developed clavus and the three-segmented tarsi; and if we place them within the Auchenorrhyncha by expanding the definition of the group to include insects with multi-segmented antennae, we would be abolishing one of the outstanding characteristics of the division. I believe, therefore, that these Lower Permian species require the erection of a third group or division, analogous with the Sternorrhyncha and Auchenorrhyncha, but combining their primitive features: long antennae, with about twenty-five segments; three-segmented tarsi; and a fully-developed clavus in each tegmen, with two anal veins. For this new division I propose the term *Paleorrhyncha.*

FAMILY ARCHESCYTINIDAE.

Subcosta entire, parallel to R1; R1 forked distally, a weak pterostigma included between the branches; Rs unbranched, arising at a point about one-half the wing length from the base; M weak, fused with R for a short distance basally and forming distally three branches; Cu dividing into Cu1 and Cu2 close to the base; Cu1 diverging abruptly near the base towards M and fusing with it for a very short distance; Cu1 usually forked distally, sometimes unbranched; Cu2 unbranched; 1A close to Cu2, terminating on posterior margin; 2A remote from 1A; clavus broad and well developed, extending nearly to the middle of the wing. Hind wing unknown.

The body is known only in the genus Archescytina, but it is probably similar in the other genera; the tarsi are three-segmented; the beak is very long and well developed; and the antennae are slenderly filiform, possessing about 25 segments.

Archescytina Tillyard.

Archescytina Tillyard, this Journal, 11, 385, 1926.

Tegmen: anterior margin slightly convex; Sc remote from R1, weakly developed; R+M arched upwards at the base, almost touching Sc; free piece of Cu1 at base directed anteriorly, so that it meets M at its very origin; Cu1 forked distally; 1A sigmoidally curved; two cross-veins, one (*rm*) between M and Rs, the other (*mcu*) between Cu1 and M3+4.

Genotype: *Archescytina permiana* Till.

Archescytina permiana Till.

Fig. 1.

Archescytina permiana Till., this Journal, 11, 386, 1926.

Tegmen: length, 8 mm.; width, 3 mm. Rs arising midway between the origin of M and the fork of R1; cell between Cu1a and Cu1b very high; Cu1b meeting the posterior margin at nearly a right angle; Cu2 terminating midway between 1A and Cu1b.

Holotype: No. 511b, Peabody Museum, Yale University; counterpart in the Tillyard collection.

In the Sellards collection there is a finely preserved tegmen of this species: No. 702, collected by Dr. E. H. Sellards at the Elmo locality. In the Harvard collection there are three specimens, collected by the writer in 1927. No. 3137 is a complete tegmen, and No. 3120ab consists of the apical part of a tegmen, not very well preserved. No. 3136ab includes parts of a tegmen; a twisted hind wing, the venation of which cannot be discerned; and part of the body, which is seen in a lateral position. One antenna (Fig. 1-D) is completely and clearly preserved except for the very base, which has flaked off the matrix. The segments are distinct in most places and number about twenty-five, probably more. Unfortunately, because of the absence of the basal segment or segments, we cannot determine just where the antenna joins the head. The anterior half of the head is preserved, showing a

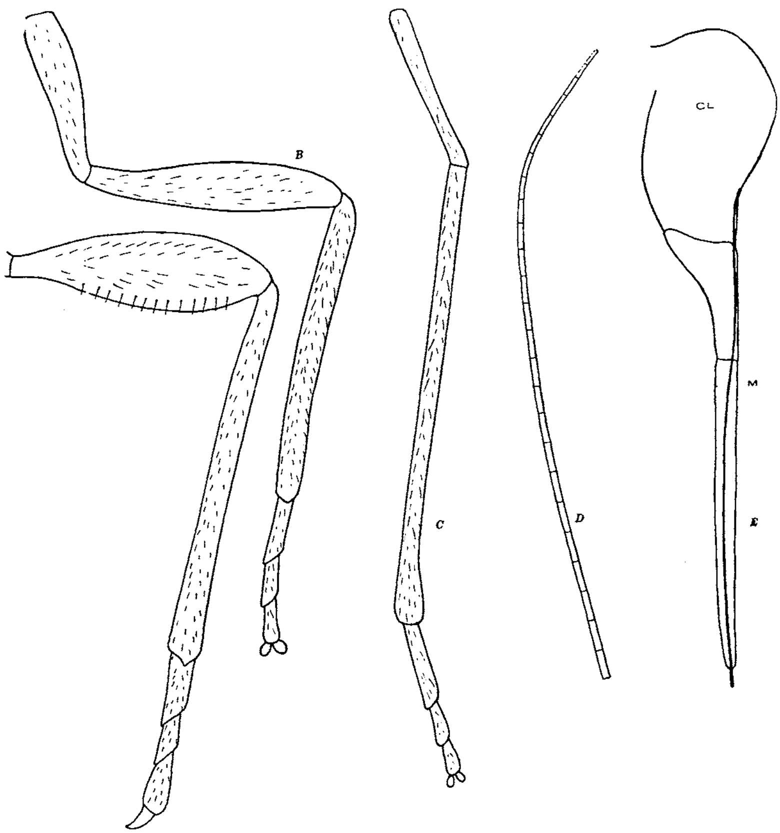

Fig. 1. *Archescytina permiana* Till. A, fore leg; B, middle leg; C, hind leg; D, antenna; E, rostrum (cl, clypeus; M, stylet). Drawn from specimen No. 3122ab, Museum Comparative Zoology.

prominent clypeus and a large beak, much like those of the Cicadidae and Cercopidae (Fig. 1-E); the posterior half of the head, including the eyes, is obscured by the prothoracic legs, which are folded upwards. The rostrum appears to arise in a manner not unlike that in the cicadas and it is fully as long as that of these insects. I can discern only two segments distinctly, a long distal one and a shorter basal piece; but there may be several subdivisions of the supposed distal segment which cannot be seen. The mandibles and maxillae are obviously modified as in recent Homoptera, appearing as a dark line (stylet), extending down from the clypeus, through the rostrum, and protruding beyond the labrum (Fig. 1-E, M); in all probability these ancient Homoptera were able to extend or retract the stylets like many modern species. The fore legs are finely preserved, except for the coxae and the trochanters. The femur is short and swollen, and bears a single row of stout bristles along the inner margin (Fig. 1-A). The tibia is narrow and long, without spines; the tarsus is composed of three subequal segments and seems to terminate in a single, stout claw, although the appearance of a single claw may be due to the position in which the leg rests. The femur of the middle leg is longer and more slender than that of the fore pair and is without spines (Fig. 1-B); the tibia and tarsus are similar to those of the fore legs, except for the last tarsal segment, which terminates in a pair of flattened claws. The hind legs are elongate and slender; the tibia is swollen slightly at its distal end; the tarsus is like that of the middle legs, but the basal segment is longer (Fig. 1-C). The thorax and abdomen are not distinctly enough preserved to show definite structures or segmentation.

Permoscytina Tillyard.

Permoscytina Tillyard, this Journal, 11, 387, 1926.

Tegmen: anterior margin slightly convex; Sc very close to Rl, strongly chitinized; R+M straight or nearly so; free piece of Cu1 at base directed apically, joining M below its origin; Cu1 forked distally; 1A sigmoidally curved.

Genotype: *Permoscytina kansasensis* Tillyard.

Permoscytina kansasensis Till.

Permoscytina kansasensis Till., this Journal, 11, 388, 1926.

Tegmen: length, 11-12 mm.; width, 3.5 mm. Costal space narrow; Sc and R1 nearly straight; pterostigma very narrow; Rs terminating at the apex of the wing; free piece of Cu1 at the base almost parallel to the axis of the wing; Cu2 terminating midway between the ends of 1A and Cu1b.

Holotype: No. 5112, Peabody Museum. In the Harvard collection there is one specimen (No. 3121ab) of this species, consisting of a tegmen complete except for the base; its venation is identical with that of the holotype.

Permoscytina muiri Till.

Permoscytina muiri Till., this Journal, 11, 389, 1926.

Tegmen: length, 11-12 mm.; width, 4 mm.; costal space broad; Sc and R1 with a distinct bend at the origin of M; pterostigma rather broad; Rs terminating anteriorly to the apex of the wing; free piece of Cu1 directed anteriorly slightly; Cu2 terminating much nearer to 1A than to Cu1b.

Holotype: No. 5113, Peabody Museum. In the Harvard collection there is a nearly complete tegmen of this species (No. 3122ab). The base of the tegmen of the holotype was covered by a flake of the limestone when Tillyard examined it; with Dr. Dunbar's permission I removed this fragment of rock, exposing the rest of the wing. This exposed portion shows that the cubitus curves upwards at the base and fuses with the media.

Paleoscytina, new genus.

Allied to Archescytina. Tegmen: anterior margin smoothly convex; Sc close to R1, weakly chitinized; R+M slightly arched; free piece of Cu1 at base directed anteriorly, fusing with M at its origin; Cu1 simple.

Genotype: *Paleoscytina brevistigma*, n. sp.

Fig. 2.

Tegmen: length, 3 mm.; width, 1 mm.; costal space very broad; pterostigma short; first fork of M basad of R1a; cross-vein *rm* distad of separation of M1 and M2; termination of 1A closer to Cu2 than to 2A.

Holotype: No. 3133ab, Museum of Comparative Zoology; collector, F. M. Carpenter. On the opposite surface of the piece of rock containing this wing there is a tegmen of *Permoscytina muiri* Till.

This minute wing is the most perfectly preserved of all the Homoptera which have been found in the Kansan Permian. The unbranched Cu1 is a specialization not found in the other Kansan species or in any other Permian Homopteran, although it does occur in many recent species, such as the cicadellids.

Permopsylla Tillyard.

Permopsylla Tillyard, this Journal, 11, 390, 1926.

Tegmen: anterior margin concave opposite origin of M; Sc close to R1, weakly chitinized; R+M slightly arched; free piece of Cu1 at base directed anteriorly, fusing with M at its origin; 1A straight; Cu1 forked distally.

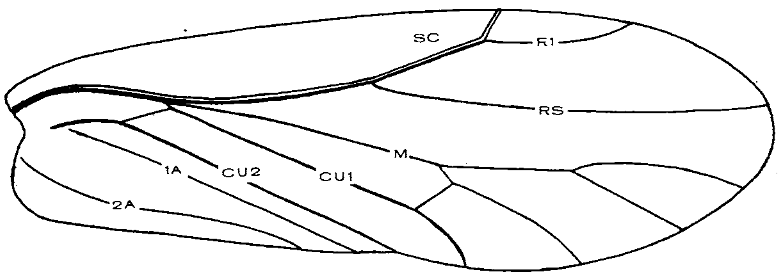

Fig. 2. Tegmen of *Paleoscytina brevistigma,* n. sp.; drawn from holotype.

Genotype: *Permopsylla americana* Till.

This genus was placed by Tillyard in a separate family, Permopsyllidae, because of the apparent reduction of the clavus. This condition of the anal area, as I have shown above, was really due to the incomplete preservation of the type specimen and was not a characteristic of the insect itself. Accordingly, Permopsylla lies well within the family Archescytinidae and is more closely related to Archescytina than to Permoscytina.[1]

Permopsylla americana Till.

Fig. 3.

Permopsylla americana Till., this Journal, 11, 391, 1926.

Tegmen: length, 3.5 mm.; width, 1.5 mm.; first fork of M below termination of R1a; cross-vein *rm* basad of separation of M1 and M2; cell between Cu1a and Cu1b about as high as long.

Holotype: No. 5114ab, Peabody Museum, Yale University.

In the Harvard collection there are three good tegmina of this insect: No. 3123ab, 3124ab, 3125ab; specimens Nos. 3126-

[1] The genera Protopsyllidium, Permopsyllidium, and Proethea, which Tillyard described from the Australian Permian and placed in the family Permopsyllidae, now require the new family name Protopsyllidiidae.

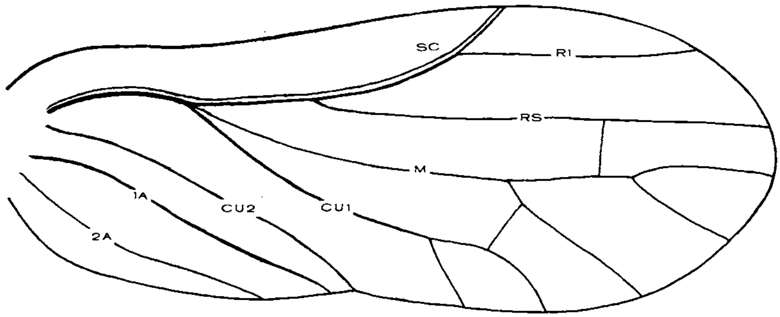

Fig. 3. Tegmen of *Permopsylla americana* Till.

3128, 3134ab also belong here, but they are more poorly preserved. The holotype of this species lacks the terminal part of Cu1 and all of Cu2 and the anal area, but these parts are preserved in the Harvard fossils.

Permopsylla permiana, n. sp.

Fig. 4.

Tegmen: length, 4 mm.; width, 1.8 mm.; first fork of M below termination of R1a; cross-vein *rm* distad of separation of M1 and M2; cell between Cu1a and Cu1b narrowly triangular.

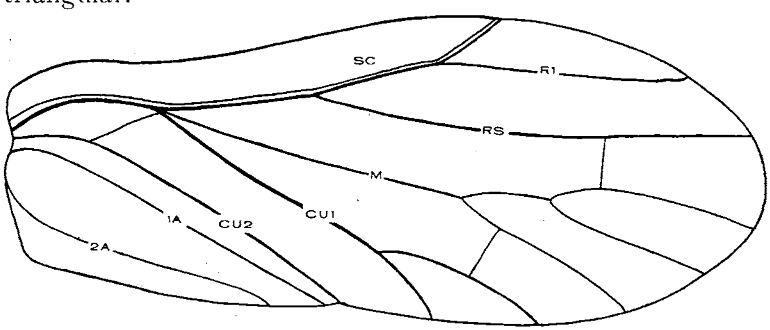

Fig. 4. Tegmen of *Permopsylla permiana*, n. sp.; drawn from holotype.

Holotype: No. 3129ab, Museum of Comparative Zoology, consisting of a complete and clearly preserved tegmen; collected by F. M. Carpenter at the Elmo locality. Paratype: No. 3130ab, Museum Comparative Zoology, also a complete tegmen, similar in venation to the holotype; collected by W. S.

Creighton. Specimen No. 3131ab belongs to this species, but the base of the tegmen is missing. *Permiana* is close to *americana*, but I believe that the deeper fork of M1+M2 and the difference in the shape of the cubital cell require specific distinction.

Permopsylla minuta, n. sp.

Fig. 5.

Tegmen: length, 2.3 mm.; width, 1 mm.; first fork of M below middle of pterostigma; cross-vein *rm* basad of separation of M1+M2; cell between Cu1a and Cu1b about three times as long as high.

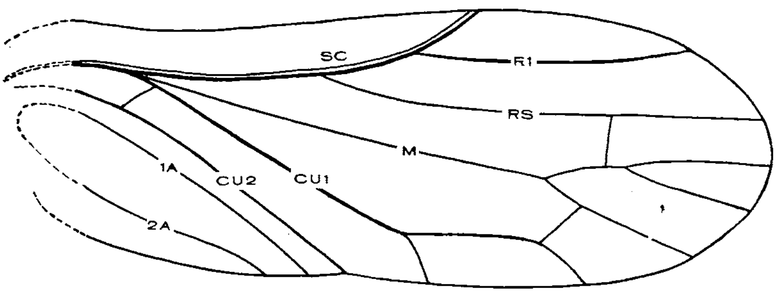

Fig. 5. Tegmen of *Permopsylla minuta*, n. sp.; drawn from holotype.

Holotype: No. 3132ab, Museum of Comparative Zoology, consisting of a complete tegmen, with very clear veins; collected by F. M. Carptenter. This is the smallest of the Kansan Permian Homoptera, but it is similar to the other species of Permopsylla except for the features noted.

These Lower Permian Homoptera, although few in number, are particularly significant because they are the oldest known representatives of the order Hemiptera.[2] The discovery of the body parts described above throws considerable light on the antiquity of the Sternorrhyncha and the Auchenorrhyncha, and requires us to abandon Tillyard's conclusions on the relationship of these two divisions. For Tillyard was led to believe from the incomplete tegmen of *Permopsylla americana*

[2] Lameere, in his revision of the Carboniferous insects of Commentry (Bull. Mus. Nat. Hist. Paris, 23: 183, 1917), regards *Dictyocicada antiqua* Brongn. as a true Homopteron, but I am unable to see enough evidence in the figures of this poorly preserved fossil to justify his conclusion.

in the Yale collection that even in the Lower Permian the Sternorrhyncha were already differentiated from the Auchenorrhyncha by several features, such as the reduced clavus and the loss of the anal veins. The new fossils, however, demonstrate conclusively that this Lower Permian species cannot be assigned to either the Sternorrhyncha or Auchenorrhyncha, and that so far as we know at present neither of these groups were in existence during the Lower Permian. The new division Paleorrhyncha, in which I have placed the Kansan fossils, combine the primitive features of the Sternorrhyncha and Auchenorrhyncha and may, therefore, be considered as the common ancestor of the two existing divisions.

When we compare the Lower Permian Homoptera with those of the late Permian of Russia and Australia, we note at once that the Kansan species are by far the most primitive, as we should naturally expect. The fifteen species described from the Russian Permian are alike in the possession of a large clavus with two anal veins, and the development of a coriaceous tegmen with distinct pittings similar to those of many existing Homoptera. There is no indication of the presence of Sternorrhynchous species. The Australian Permian has yielded twenty-six species of Homoptera, most of which are similar in general features to the Russian insects. But there are six species which Tillyard referred to the Sternorrhyncha. Most of the specimens on which these species were based lack the clavus entirely, and Tillyard inferred, as in the case of the Kansan Permopsylla, that the clavus was reduced and that the tegmen belonged to a member of the Sternorrhyncha. This conclusion is perhaps open to question, and one of the two specimens with the clavus preserved shows two anal veins, as in the Auchenorrhyncha. I believe, therefore, that we do not have sufficient evidence to justify the statement that the Sternorrhyncha were present during the Permian or even that Homoptera with the venational characteristics of the Sternorrhyncha existed then.

Since the Elmo limestone is far down in the lower part of the Permian formation, the reduced wing venation and particularly the perfect, well-developed rostrum of the Kansan Homoptera are positive proof that the order Hemiptera arose in the Carboniferous. Our knowledge of the small insects of the Carboniferous is negligible and there is apparently no fossil known from that horizon which shows affinities with the

Homoptera. But these Kansan fossils, although well along the Homopterous line of descent, substantiate certain views which have previously been advanced on the relationship between the Psocoptera and the Homoptera. Crampton has emphasized the apparent relationship between the two orders in several papers (1922, 1927), and Tillyard has also concluded that the Homoptera arose with the psocids from a common ancestral stem.

Any inquiry into the relationship of the Homoptera with other insects naturally introduces the question of the origin and relationship of the Heteroptera. At the present time a total of forty-seven species of Hemiptera have been described from the Permian strata of both hemispheres, and all of them belong to the Homoptera, the earliest Heteroptera occurring in the Triassic of Queensland (Tillyard, 1918). The persistent absence of Heteroptera from Permian beds thus far is strongly suggestive that the suborder was not in existence at that time, although such evidence is purely negative and should not be regarded as proof of such a thesis. The question of the origin of the Heteroptera has become especially complicated because of the discovery of several large insects with prominent beaks in the Carboniferous rocks of Commentry, France. These fossils, of which Eugereon is the best representative, were placed by Handlirsch (1906) in a separate order, Protohemiptera, and considered ancestral to the Hemiptera as a whole, a view which has been generally accepted by most students of insect phylogeny. In 1924 Martynov noted a few objections to the idea that Eugereon was a relative of the Hemiptera and in 1927 Crampton treated the subject very thoroughly, demonstrating conclusively that Eugereon could not be regarded in such a position. Both Crampton and Martynov agree that Eugereon shows closest affinities with the Paleodictyoptera, and probably represents an end group which was derived from that order.

ADDITIONS TO PALEODICTYOPTERA.

Since the publication of the previous paper in this series, additional specimens have been found belonging to certain orders already treated. These new fossils were secured by breaking up fragments of the Elmo limestone which had been sawed from large pieces of the rock containing other fossils. One of the new specimens is a Paleodictyopteron and is of considerable interest, for it is only the second Permian species of the order known,[3] the other being *Dunbaria fascipennis* Till., from the same locality. The new species is more highly specialized than Dunbaria and requires the erection of a new family.

PERMONEURIDAE, new family.

Hind wing with an enlarged anal area; costal margin serrated; R1 unbranched, Rs with numerous branches; MA fused with Rs for most of its length; Cu1 absent; only two anals present.

Permoneura, new genus.

Small insects. Hind wing: costal area rather broad, but without veinlets; Sc extending nearly to the apex of the wing; Rs arising well before the middle of the wing; M close to R at base; free piece of MA at base very short, almost parallel to the longitudinal axis of the wing; Cu2 removed from both M and 1A.

Genotype: *Permoneura lameerei*, new species.

Permoneura lameerei, n. sp.

Fig. 6.

Hind wing: length, 10 mm.; width, 4 mm.; Sc very close to R1, terminating just above it; Rs diverging from R1 rather obliquely, but after fusing with MA, it makes an abrupt bend and continues almost parallel to R1; Rs with 7 branches, equally spaced; MA directed obliquely away from R at base, MA and MP separating just a little distad of the origin of Rs; MP with 3 branches, M1+M2 unbranched, originating just below the point of fusion of Rs and MA; Cu2 with three distal branches; 1A unbranched; 2A forked distally, and connected to the inner margin of the wing by another short branch. There are apparently no cross-veins, but the wing membrane was undoubtedly supported by the fine network which characterized the Paleodictyoptera.

Holotype: No. 3135ab, Museum of Comparative Zoology; collected by F. M. Carpenter. The species is named for Professor Auguste Lameere, of the University of Bruxelles, in recognition of his researches on fossil insects.

[3] Excluding two very doubtful fragments which Martynov has described from the Russian Permian.

This well-preserved fossil is obviously a hind wing, with the convexities and concavities of the veins strongly marked. The ordinal position of the wing seems at first sight rather dubious, because of several remarkable features not unusually attributed to the Paleodictyoptera. The serrated costal margin and the structure of Sc, R1, and Rs are characteristic of the order, but the media, cubitus and the anal veins are peculiarly modified. The obverse half of the fossil can easily be recognized by the concavity of Sc and Rs, and the convexity of

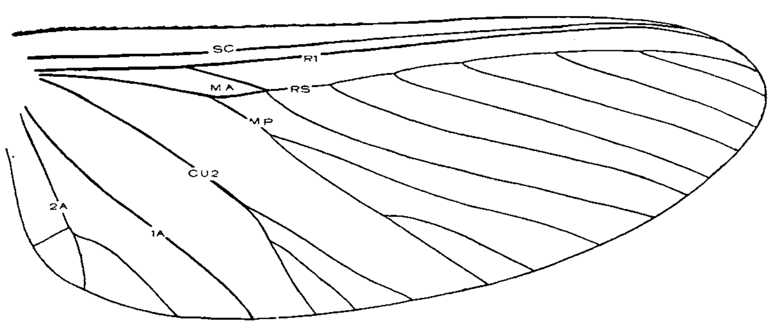

Fig. 6. Hind wing of *Permoneura lameerei*, n. sp.; drawn from holotype. Sc, subcosta (—); R1, radius proper (+); Rs, radial sector (—); MA, anterior media (+); MP, posterior media (—); Cu2, second cubitus (—); 1A, 2A, anal veins.

R1.[4] In this half the media is distinctly concave and must, therefore, be the posterior media (MP). The anterior media (MA) is apparently fused with Rs and is present as a free vein only at the base before this coalescence takes place. The next vein posteriorly, obviously the cubitus, is also concave and hence must be Cu2, Cu1 being absent. The reduction of MA and the complete absence of Cu1 would seem at first thought to eliminate this insect from the Paleodictyoptera, which are supposed to have possessed a full system of veins. In 1922 Lameere published an instructive account of the wing venation of these insects, and if I interpret his remarks correctly, he believes that all Paleodictyoptera possessed both the anterior and posterior media, as well as Cu1(+) and Cu2(−). Tillyard seems to have taken this view also in his discussion of

[4] In this connection I wish to call attention to a confusing misprint on page 363 of Part 3 of this series (Psyche 37. 1930): in line 26 the words "convex" and "concave" should be interchanged.

Dunbaria. Unfortunately, by far most of the known Paleodictyoptera were described before the significance of the convexities and concavities of the veins was realized, so that very little is known of this aspect of the venation in the order as a whole. But during the past few years I have examined a number of type specimens of Paleodictyoptera, many from Mazon Creek, Illinois, and I have observed that the anterior media is frequently absent, as well as Cu1, although in other respects the insects are typical Paleodictyoptera and have been

Fig. 7. *Doter minor* Sell.; photograph of specimen No. 3059ab, Museum of Comparative Zoology.

placed in that order by Handlirsch and others. Consequently, the reduction of MA and the absence of Cu1 in *Permoneura* does not exclude that insect from the Paleodictyoptera. Of course, as defined at present, the order includes a heterogeneous mixture of related and unrelated insects and I do not believe that Handlirsch's classification is a natural one; but until all the described specimens have been reëxamined with especial reference to the convexity and concavity of the veins, a satisfactory division of the "order" cannot be reached.

ADDITIONS TO PROTOHYMENOPTERA.

Six new specimens of Protohymenoptera were also obtained in the same manner as *Permoneura*. Five of these consist mainly of wings and deserve little comment, one being *Protohymen permianus* Till., and the others *Doter minor* Sell. (Nos. 3116-3119). The sixth specimen (No. 3059ab), which also belongs to the latter species, is of much greater interest, since it shows a structure which has not previously been found in any Paleozoic insect,—a well-developed ovipositor. The insect rests in a lateral position (Fig. 7), with the abdomen slightly arched. When I found the fossil, the finely-preserved wings were placed over the abdomen, but having observed that the distal part of the abdomen was very clear, I decided to chip away the wings with the hope of exposing more of the abdomen. This operation was successful, for, as shown in the photograph, I was able to uncover all but the very base of the abdomen. On the same fragment of rock and only about a centimeter away from this fossil, there is a specimen of a may-fly (Protereisma), one of the legs of which lies across the very end of the abdomen of the Protohymenopteron. Most of the leg was also chipped away, but some of it still remains, as shown in the photograph, and should not be confused with the cerci.

The abdomen terminates in the basal segments of the two cerci, the rest of which are not preserved, although I have already described them from another specimen in the foregoing paper of this series. The last abdominal segment is small and consists of both sternites and tergites (Fig. 8). The next segment basad is much larger, the tergite apparently covering the whole side of the segment, and the sternite visible only along the ventral edge. The remaining abdominal segments are nearly uniform in size, the tergites extending almost to the middle of the sides. Unfortunately, the obscurity of the base of the abdomen prevents us from counting the number of segments, but for reasons which I shall discuss below, I am inclined to believe that the cerci arise from the 11th segment. The ovipositor itself is splendidly preserved, but, of course, it is impossible to trace the basal origins of the several parts, for even in recent insects the basal connections of the various processes cannot usually be determined without subjecting the insect to a certain amount of dissection or treatment with solvents. In our Protohymenopteron the lower appendage is the longest, extending well beyond the basal segments of the cerci, and it is somewhat dilated distally. Just above this process and arising slightly distad to it, there is a shorter appendage, which terminates before the end of the abdomen. I do not discern any indication of another process, although the structure which I have considered the sternite of the 10th segment may be another one of the gonopophyses, pressed against the abdomen.

Now in recent insects the ovipositor is usually regarded as consisting of three pairs of gonopophyses: the ventral valves, which arise from the 8th abdominal segment; the internal valves, which arise from the 9th segment; and the dorsal valves, which also originate from the 9th segment. There can be no doubt that the lower appendage in the Protohymenopteron is the ventral valve and that it arises from the 8th seg-

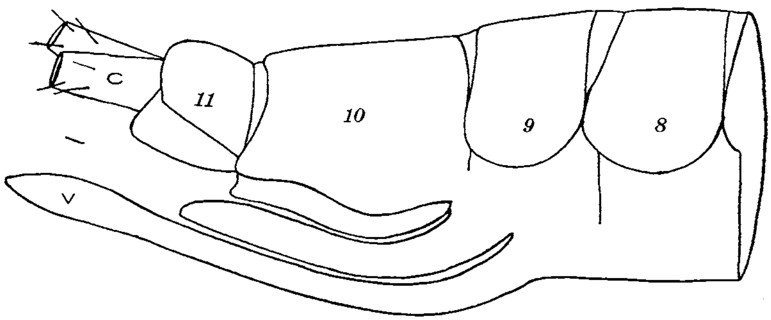

Fig. 8. *Doter minor* Sell.; Terminal part of abdomen, drawn from specimen No. 3059ab. C, cerci; V, ventral valve; 8, 9, 10, 11, abdominal segments.

ment. The other process may correspond to either the inner valve or the dorsal valve; in recent insects the dorsal valve is usually the larger of the two, the inner valve being concealed within, and that may be the arrangement in the fossil. In those recent insects which possess such an ovipositor the ventral valves have the appearance of arising from the 9th segment instead of the 8th, and the other valves seem to have been thrust distad also. The fossil shows this same condition: the ventral valve appears to arise from the middle of a segment. I therefore believe that we are justified in assuming that the ventral valve actually arises from the next segment basad, the fourth from the end, which should be the 8th, inasmuch as the ventral valves arise from that segment in recent insects. If this is the case, then there are eleven segments to the abdomen, unless we choose to regard what appears to be the terminal segment as formed from certain modified plates of the 10th.

Aside from these morphological and perhaps somewhat doubtful questions, the presence of a well-developed ovipositor in Doter is interesting because it is the first unquestionable instance of such a structure in a paleozoic insect. The obscure *Dieconeura arcuata* Scudder, from the Carboniferous nodules of Mazon Creek, Illinois, is supposed by Handlirsch to have possessed some sort of an ovipositor, as shown in his restoration of the insect. But no such appendage was observed by Scudder in his original figure or description of the fossil, and I was unable to find one when I examined the type specimen at the National Museum in 1926. Tillyard has described what he considered to be an ovipositor in one of the psocids from the Lower Permian of Kansas, but if the structure which he indicates really represents an ovipositor, it is weakly developed and certainly not comparable with that of Doter. The Paleodictyopteron *Lycocercus goldenbergi* Brongn., from the Carboniferous of Commentry, possesses a pair of independent, broad plates attached near the end of the abdomen. These may represent some form of genital armature, as suggested by Brongniart, Lameere, and Handlirsch, but they do not resemble an ovipositor. The gonapophyses of Doter, however, undoubtedly form a true ovipositor and signify that at least by the time of the Lower Permian oviposition had become specialized in at least one group of insects. I do not believe that the discovery of this structure in the Protohymenoptera aids us in any way to determine more definitely the affinities of the group with recent insects. An ovipositor occurs in a great many unrelated insect orders, so that its mere presence would be of little phylogenetic significance, and we do not know enough of the detailed structure of the Protohymenopterous ovipositor to enable us to go further into the question.

Museum of Comparative Zoölogy,
Cambridge, Mass.

BIBLIOGRAPHY.

Carpenter, F. M.

1930. The Lower Permian insects of Kansas. Part 1, Introduction and the order Mecoptera. Bull. Mus. Comp. Zool., 70 (2): 69-101.

1931a. The Lower Permian insects of Kansas. Part 2, The orders Paleodictyoptera, Protodonata, and Odonata. This Journal, 21, 97-139.

1931b. The Lower Permian insects of Kansas. Part 3, the Protohymenoptera. Psyche, 37 (4): 343-374 (1930).

CRAMPTON, G. C.

1922. Evidence of relationship indicated by the venation of the fore wing of certain insects, with especial reference to the Hemiptera-Homoptera. Psyche, **29** (1) : 23-41.

1927. Eugereon and the ancestry of the Hemiptera, Psocids, and Hymenoptera. Bull. Brookl. Ent. Soc., **22** (1) : 1-17.

MARTYNOV, A. V.

1924. The interpretation of the wing veins and tracheation of the Odonata and Agnatha. (Russian). Rev. Russe. Ent. Soc., **18**: 145-174. English translation in Psyche, **37** (3) : 245-280, 1930.

1928. The Permian fossil insects of North-East Europe. Trav. Mus. Géol. Acad. Sci. URSS, **4**: 1-118.

LAMEERE, A.

1922. Sur la nervation alaire des insectes. Bull. Sci. Acad. Roy. Belg., **1922**: 38-49.

TILLYARD, R. J.

1918. Mesozoic insects of Queensland. Part 4, Hemiptera Heteroptera. Proc. Linn. Soc. N. S. W., **43**: 567-592.

1926a. Kansas Permian insects. Part 9, the order Hemiptera. This Journal, **11**: 381-395.

1926b. Upper Permian insects of New South Wales. Part I. Introduction and the order Hemiptera. Proc. Linn. Soc. N. S. W., **51** (2) : 1-30.