

Proceedings of the American Academy of Arts and Sciences

VOL. 73, No. 3, P. 29-70—MARCH, 1939

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PROTELYTROPTERA, PLECTOPTERA, AND PROTOPERLARIA

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Received February 15, 1938

Presented March 9, 1938

In the summer and fall of 1935, a few months after the previous part of this series of papers was published, the writer made another trip to the Lower Permian limestone at Elmo, Kansas, and secured several thousand more insects for the Museum of Comparative Zoölogy. The Museum collection from this formation now exceeds eight thousand specimens.

The new fossils were found in the same quarry which yielded the 1932 material. At this quarry, as I have previously indicated (1933, p. 411; pl. 1, fig. 1), the insect-bearing limestone occurs in two layers, separated by a thin bed of soft calcareous shale. The new collection therefore includes specimens from both layers, though the majority of them were found in the upper one. The quarry was worked eastward, i. e., in the direction in which the photograph already mentioned was taken. At a distance of about 15 feet from the front of the quarry a noticeable decrease in the thickness of the limestone was apparent. This diminution took place in both layers and became more pronounced as the quarry was developed further eastward, so that at a distance of about twenty feet from the starting point, the limestone was entirely absent (Plate 1, fig. 1). I have previously called attention to the apparent lenticular nature of the Elmo limestone (1933, p. 412), but this new exposure is the first one actually to reveal the edge of one of the beds. It should be noted that as the limestone thins it becomes less fossiliferous. Most of the new fossils were collected at the west end of the quarry, where both layers were very thick.

This paper deals only with those specimens contained in the 1935 collection belonging to the orders and families which I have already treated in earlier publications, namely, the Megasecoptera, Protodonata, Odonata, Homoptera, Psocoptera, Protelytroptera, Plectoptera, and Protoperlaria. There is, of course, a great deal of duplication of the species previously collected, but the new fossils add materially to our knowledge of their structure. In some instances the additional

information has made it necessary to revise our opinions of their classification and affinities. This latest collecting trip was in fact made, not with the expectation of securing many new species, but with the hope that a large series of additional fossils would show structural details formerly unknown in the species which had been found, especially of the Protohymenoptera, Odonata, and Homoptera. In this respect the results of the trip were very satisfactory, for the 1935 collection exceeds all others in the number of complete or nearly complete specimens included.

Before closing these introductory remarks, I wish to acknowledge the financial aid of two grants which made the 1935 trip possible; these were obtained from the Permanent Science Fund of the American Academy of Arts and Sciences and the Penrose Bequest of the Geological Society of America. I also acknowledge the invaluable assistance of my wife, who accompanied me on the trip and found a large proportion of the new fossils. As on former occasions we are indebted to Mr. and Mrs. E. E. Bert and Miss Rowena Bert for their kindness during our stay in Abilene; and to Paul and Joseph Bert for their assistance in the field.

Order MEGASECOPTERA

Suborder Protohymenoptera

Some of the most interesting fossils collected in 1935 are members of the group which Tillyard has termed the Protohymenoptera. Sixty-one new specimens of these insects were found, making a total of 143 in the Museum of Comparative Zoölogy. Forty-one of the new fossils were secured in the upper layer of the limestone, and twenty in the lower layer.

Family PROTOHYMENIDAE

Genus *Protohymen* Till.

Protohymen Tillyard, 1924, Amer. Journ. Sci., (5) 8: 113.

Protohymen Carpenter, 1930, Psyche, 37: 349.

In addition to the new species described below there are three species in the new material belonging to this genus. *Protohymen permianus* Till. is represented by four specimens, consisting entirely of single wings; two of these (Nos. 3807ab and 3809ab) were found in the upper layer, and the other two (Nos. 3808ab, 3810ab) in the lower. One specimen (No. 3811ab), consisting of the apical third of a wing and belonging to *Protohymen readi* Carp., was found in the upper layer. *Protohymen elongatus* Carp. is represented by two fossils from the upper layer (Nos. 3813ab, and 3814ab), the former being the best specimen of the wing which has yet been found. It has a venation like that of the holotype except that there are two cross-veins instead of one between 1A and the hind margin.

Protohymen tenuis, new species

Figure 1

Fore wing: length, 12 mm.; width, 2 mm.; very slender, the anterior margin not so strongly curved as in other species of the genus; R1 contiguous with the costal margin for its whole length; no cross-vein between R1 and Rs proximal of the pterostigma; the one cross-vein between Rs and MA is distal of the fork of Rs; Cu1 coalescing with the stem of M, as in other species of the family; MP separating from Cu1 at a point remote from the base of the wing, well distad of the first cross-vein between Cu1 and Cu2; 3 cross-veins between Cu1 and Cu2, but only 2 between Cu2 and 1A; 1A much shorter than in other species of *Protohymen* except *permianus*.

Hind wing unknown.

Holotype: No. 3812ab, Museum of Comparative Zoölogy; collected by the writer in the lower layer of limestone at Elmo in 1935.

This wing is the most tenuous of all the known Protohymenoptera. In many venational features, as well as in shape, the wing approaches that of *elongatus*; but it is so much smaller than *elongatus* (which is 19 mm. long) and possesses such a distinctly shorter 1A that I am convinced it represents a distinct species.

Genus *Permohymen* Till.

Permohymen schucherti Till.

Figure 2A

Permohymen schucherti Tillyard, 1924, Amer. Journ. Sci., (5) 8: 116.

Permohymen schucherti Carpenter, 1936, Psyche, 37: 354.

Five specimens of this species were found in 1934. Three of these (No. 3816, lower layer; No. 3817, upper layer; No. 3818, lower layer) consist of wings only, but the other two show various parts of the body. Since nothing has previously been known about the body structure of *Permohymen*, the latter specimens are of particular interest. One of them (No. 3815ab, upper layer) shows the abdomen and part of the thorax in lateral view, as well as one complete wing; this specimen has an ovipositor, much like that already described in *Asthenohymen* (Carpenter, 1932), although the details of the various parts cannot be distinguished. The presence of the ovipositor in *schucherti* has much significance, since it demonstrates that *Asthenohymen* was not the only genus of the Protohymenoptera to possess this structure. In all probability an ovipositor also existed in *Protohymen*.

The other specimen of *Permohymen schucherti* (No. 3819ab, upper layer) is of even more interest, since it consists of almost the whole insect, although the legs, cerci and details of the head are not preserved. The dimensions of this specimen are as follows: length of entire body, 8 mm.; head, 1 mm. long, 1.5 mm. wide; thorax, 3 mm. long, 2.5 mm. wide; abdomen, 4 mm. long, 2 mm. wide. Since the wing is 10 mm. long, the abdomen is proportionally much shorter than in *Asthenohymen*. The most striking feature of this specimen is the genitalia, which are obviously those of a male. They consist of a pair of large claspers about 2 mm. long and a pair of much smaller processes nearer the median axis of the abdomen (Figure 2A). These genital structures are strikingly similar to those of the existing may-flies (Figure 2B), the two claspers obviously being the homologues of the styli of the may-flies. Like the latter structures the claspers in *Protohymen* are apparently "jointed" near the middle, though they lack the distal false-segments of plectopterous styli. The distal piece of each of the claspers bears distinct impressions of blunt teeth or tubercles along the inner margin. The two inner processes are apparently the homologues of the paired penes of the may-flies; at any rate no other interpretation of them has occurred to me. The presence of paired penes in *Protohymen* is especially interesting, for the only Recent insects with such structures are the Plectoptera and some Dermaptera.¹ The significance of the

¹ According to Snodgrass (1936) the lateral gonoducts of the male have separate openings, perhaps second-

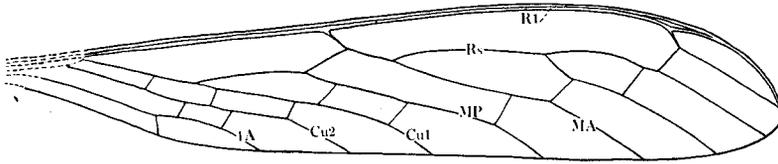


FIGURE 1. *Protohymen tenuis*, n. sp., drawing of fore wing; holotype, No. 3812ab, Museum of Comparative Zoology.

paired penes in these two orders is uncertain. Snodgrass is of the opinion that there is no specific evidence of the production of a median intro-mittent organ by the union of paired penes in any insects other than the Dermaptera and Plectoptera, and that in these two orders a union of the penes has taken place quite independently. The presence of the paired penes in *Protohymen* may not, therefore, have any phylogenetic significance, but it does suggest a relationship between the Protohymenoptera and the Plectopteran ances-

on several of the abdominal segments. These may be vestiges of gills, similar to those which occur in the Palaeodicyoptera and Protoperlaria, but I think it more probable that they are only flaring lateral margins like those of some existing may-flies (e. g., *Siphonisca acrodromia*).

Family ASTHENOHYMENIDAE

Genus *Asthenohymen* Till.

Forty-seven specimens of species belonging to this genus were collected in 1935. Most of these belong to *dunbari* or *pusillus*, but one excellent wing is referable to *affinis*.

Asthenohymen dunbari Till.

Figure 3

Asthenohymen dunbari Tillyard, 1924, Amer. Journ. Sci., (5) 8: 117.

Doter minor Carpenter (nec Sellards), 1930, Psyche, 37: 360.

Thirty-two specimens were found in 1935, eleven from the lower layer, the rest from the upper layer. Four of these specimens are of much interest since they present enough of the body structure to enable us for the first time to make a complete reconstruction of the insect and to determine the differences between the fore and hind wings. Specimen No. 3821ab (lower layer) is a lateral view of the whole insect and shows the head particularly well. No. 3820 (upper layer) is also a lateral view of the whole specimen, the head and ovipositor being well preserved. No. 3822ab (lower layer) shows an oblique view of head, but a lateral view of the rest of the body; the cerci are complete and are 12 mm. long. No. 3823ab (lower layer) is a dorsal view of a whole specimen, showing especially well the habitus of the insect.

In previous papers (1930, 1931) I have already described the legs, antennae, and the terminal part of the female abdomen, including the ovipositor. With the addition of the new material, it is now possible to give a fairly complete account of the body structure of this insect. The body as

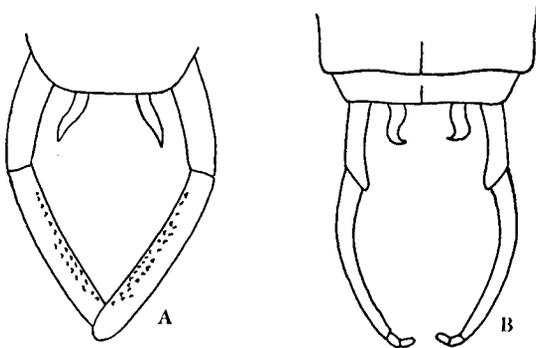


FIGURE 2. A. *Permohymen schucherti* Till., drawing of male genitalia; specimen No. 3819ab, Museum of Comparative Zoology. B. *Hexagenia* sp. (Recent, Plectoptera), drawing of male genitalia.

tors.² This is quite in accordance with the view that the Protohymenoptera are megasecopterous, since the Plectoptera have been generally regarded as part of the complex which also consists of the Odonata, Megasecoptera, and Proto-donata.

This same specimen of *Permohymen schucherti* (No. 3819ab) also shows small lateral processes

arily, in certain Diptera. The Protura also have separate openings, but these arthropods are not consistently regarded as insects, and their bifid organ is apparently not homologous with the penes of insects.

² It is pertinent to note that the male genitalia of the Permian may-flies (Permioleptoptera) are very similar to those of the Recent ones, although the penes of the Permian species have not yet been seen.

a whole was slender, and the abdomen was nearly as long as the wings, so that when the insect was at rest, with the wings folded back over the body, the abdomen proper projected slightly beyond the wing tips. The antennae were about two-thirds as long as the wings (3.5 mm. in specimen No. 3115ab), and contained almost 35 segments, the two proximal ones being much larger than the others (No. 3115ab, 3823). The head, seen from above, was rounded, with prominent but apparently not bulging eyes. The most extraordinary feature of the head has only now been brought to light by the new specimens: the prolongation of the head into a rostrum, resembling that of *Panorpa* (Mecoptera). This beak is not, of course, visible in specimens showing dorsal or ventral views of the insect; it can be distinguished only in those preserved in a lateral position. Fortunately three specimens in lateral view were secured in 1935 and in each of these the beak is very distinct (Nos. 3821ab, 3820ab, 3822ab). The lateral specimen which I described and figured in 1931 (p. 127, fig. 7) also shows this beak; but the appearance given by this specimen was that part of an antenna was resting across the head in such a way as to give the impression of a rostrum. The clear preservation of a beak in three additional specimens, however, eliminates such a misinterpretation of the head structure. In specimens No. 3821ab and No. 3820ab the head and rostrum together are 1.8 mm. long; in No. 3822ab, which is a little smaller, they are 1.5 mm. long (Plate 2, fig. 2). It is not possible to identify the various mouth-parts in these specimens, and it is very probable that we shall never be able to make out these details in such small insects; but that the mouth-parts were mandibulate is hardly to be questioned. The thorax was about three times as long as the head, as seen from above, the prothorax being the smallest part (.7 mm. long in Nos. 3821ab, 3823ab). The meso- and metathoracic segments were about equal in length (1.2 mm. in No. 3821ab) and distinctly broader than the head. The legs are well preserved in a number of specimens but are particularly clear in specimens Nos. 3115ab, and 3059ab. The fore legs (length, 2 mm. in No. 3115ab) were shorter than the others; the fore femur was shorter but stouter than the tibia, and the tarsus consisted of three subequal segments. The middle legs were slightly larger than the fore pair (2.5 mm. in No. 3115ab and 3059ab), and the third tarsal segment was about twice as long as the others. The hind legs were

the longest of all (3 mm. in 3059ab), and had the tarsal structure like that of the middle pair. Small tarsal claws were present but further details of the pretarsus are not discernible. The abdomen of the female shows 11 segments visible from above; the segmentation of the abdomen has already been discussed with reference to the ovipositor (Carpenter, 1931, p. 128), and one of the 1935 specimens (No. 3823ab) bears out the earlier conclusions. The ovipositor itself is best preserved in the specimen (No. 3059ab) in which it was originally described; and it shows in lateral view in only one other specimen (No. 3820ab). Its greatest length (*i. e.*, ventral valve) is 3 mm., and it protrudes very slightly beyond the end of the 11th abdominal segment. In this connection specimen No. 3823, which is a dorsal (or ventral) view of the insect, is particularly interesting. The cerci are somewhat separated proximally in this fossil, and between the first two segments a median process is discernible. The nature of this process becomes clear when the specimen is examined under the binocular microscope with the light directed from one side of the insect; this arrangement shows very clearly the outlines of the whole ovipositor and demonstrates that this median process is the tip of the ventral valve. This is the only specimen which has thus far been found that shows the ovipositor in a dorsal-ventral view. Nothing is known so far of the male genitalia of *A. dunbari* or for that matter of any of the Asthenohymenidae. The cerci are exceedingly long in *dunbari*; their full length being 12 mm. (No. 3822ab, plate 2, fig. 2), which is about twice as long as the entire body. They contain about 88 segments, each of which bears a pair of hairs directed distally.³

So far as the wings are concerned, it is now clear from the complete specimens secured in 1935 that the hind wings were very similar to the fore, differing in minor details only. As I suggested in 1933 (p. 429) the supposed variation in the shape of the individual wings is a matter of the differences between the fore and hind pair. The fore wing has a slightly bulging costal margin near the base and a smoothly curved anal margin, whereas the hind wing has a straight costal margin

³ It should be noted that specimen No. 3822ab, which shows the complete cerci, is slightly smaller than specimen No. 3115ab, in which the cerci were originally described. This accounts for the fact that although the cerci of the former are only about 2 mm. longer than those of the latter, they contain 1/3 again as many segments.

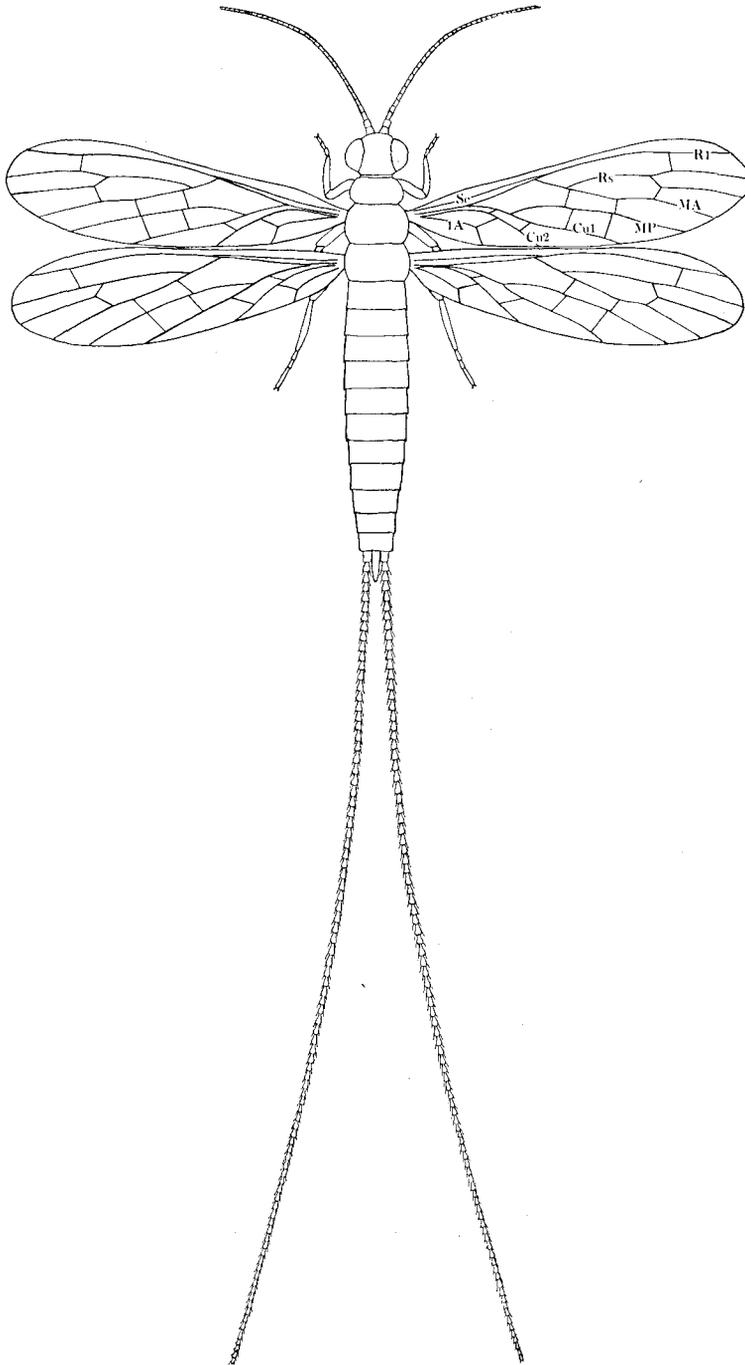


FIGURE 3. *Asthenohymen dunbari* Till., reconstruction, based mainly on specimens numbered 3820ab, 3821ab, 3822ab and 3823ab in the Museum of Comparative Zoology.

proximally and a more angular anal margin. In connection with the latter characteristic the first anal vein (1A) is somewhat shorter in the hind wing than it is in the fore.

Asthenohymen pusillus Till.

Asthenohymen pusillus Tillyard, 1926, (5) 11: 68.

Twelve specimens of this species were collected in 1935, all but one coming from the upper layer. Four of them (Nos. 3834, 3836, 3825, 3839) are especially fine wings. The differences in the fore and hind wing now known in *A. dunbari* show that the specimen of *pusillus* figured by me in 1933 (fig. 7) is a hind wing.

THE AFFINITIES OF THE PROTOHYMENOPTERA

In my first account of the Protohymenoptera (1930) I concluded from the available evidence that (1) the venation of the Protohymenoptera was incorrectly interpreted by Tillyard; (2) the Protohymenoptera were closely related to the Megasecoptera and not more than a suborder of that group; and (3) the Protohymenoptera were not ancestral to the Hymenoptera, as originally claimed by Tillyard. Although Tillyard has briefly expressed his opposition to these views (1932), it is only very recently (1936) that he has discussed the subject in detail. In this latest account he accepts the interpretation of the venation of the Protohymenoptera which I proposed in 1930 and he furthermore accepts the idea that the Protohymenoptera are very closely related to the Megasecoptera. He prefers not to regard the Protohymenoptera as a suborder of the Megasecoptera, though he states (1936, p. 450) that it is a matter of personal choice whether the group is regarded as holding subordinal or ordinal rank. He therefore admits the validity of the first and second of my conclusions regarding the Protohymenoptera, but refuses to concede that the third conclusion is correct, and in fact advances additional arguments to support his original view.

As I pointed out in 1930, in demonstrating that the Protohymenoptera are megasecopterous, we do not necessarily prove that they have no phylogenetic connection with the Hymenoptera. But if we still attempt to derive the Hymenoptera in this way, we at once remove the order from all the other holometabolous insects. This is precisely the view that Tillyard takes. He considers the Protohymenoptera to be a specialized offshoot of the common ancestor of the Megasecoptera, the Odonata and Protodonata,

so that the Hymenoptera are thus more closely related to the Odonata than to the Mecoptera, Neuroptera, and the other panorpoid orders.

In this discussion I shall not review the evidence indicating that the Hymenoptera are derivatives of the same holometabolous complex which has produced the panorpoid orders, since that is the view that is generally accepted; but I shall attempt to refute the arguments which Tillyard advances to demonstrate that the Hymenoptera are derived from Protohymenoptera. To begin with, however, Tillyard first claims that the presence of a "complete archaic ovipositor" in the Protohymenoptera (*Asthenohymen*) is proof that the Hymenoptera are not members of the same complex which produced the panorpoid orders, since "the Hymenoptera are the only group of Holometabolous insects in which such an organ is developed." This is indeed an extraordinary statement, since in two groups of Neuroptera (suborder Raphidioidea, and the family Dilaridae) a similar, complete ovipositor occurs. Furthermore, as has been pointed out by several insect morphologists (e. g., Crampton, 1929), the ovipositor of the Hymenoptera is more similar to that of the Raphidioidea than it is to that of any hemimetabolous insect (Figure 4). So instead of being evidence that the Hymenoptera are not related to the panorpoid orders, the presence of an ovipositor in the Hymenoptera is strong evidence of just that relationship.

Tillyard's arguments for deriving the Hymenoptera from the Protohymenoptera are as follows (1936), pp. 451-452):

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 cells. The same type of venation occurs in the Protohymenoptera, and the venation of the Hymenoptera can be logically derived from that of the Protohymenoptera.

4) The structure of the head, antennae, and eyes in *Asthenohymen* are such that it could easily be the ancestor of the Hymenoptera.

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 it seems reasonable to suppose that *Asthenohymen* still 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. 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.

It is obvious that the last (7th) argument is concerned with the question of the relationship between the Protohymenoptera and Megasecoptera, and not with the ancestry of the Hymenoptera. It is also clear that the 5th and 6th of these arguments are purely of a negative nature, that is, they remove certain objections which might otherwise be advanced against the descent of the Hymenoptera from the Protohymenoptera.⁴ The first and third arguments seem to me to be identical, both stating that the venation of the Hymenoptera can be interpreted logically in terms of the Protohymenoptera. But this conclusion neglects completely the question of convergent evolution of the venation, instances of which are innumerable among the insects. Furthermore the fact that Tillyard has interpreted the hymenopterous venation in two very different ways (see Tillyard, 1936, p. 448) on the basis of the assumed descent from the Protohymenoptera, and in both instances found the in-

terpretation "logical," shows that the venation of the Protohymenoptera and Hymenoptera is not so similar as one might conclude from Tillyard's arguments. The same reply can be directed against the fourth argument, that the head, antennae, and eyes in *Asthenohymen* (the only genus of Protohymenoptera in which the head structure has been known) are such that it could easily be the ancestor of the Hymenoptera. Granting that this statement were true, it would not indicate that the Hymenoptera were descended from *Asthenohymen*; it would suggest that *Asthenohymen* could have been ancestral to the Hymenoptera and nothing more. Of course when Tillyard's statement was made very little was known of the head structure of *Asthenohymen* except the antennae and form of the eyes. But the discovery of the new specimens of *Asthenohymen* described above shows that the head in this genus was very specialized in possessing a rostrum, a type of head which could obviously not have been the source of origin of the generalized head of the Hymenoptera.

Tillyard's second argument, that the wing-membrane in the Hymenoptera is hard and glassy, as it is in the Protohymenoptera, fails again to take into consideration parallel evolution, for such a wing membrane has been developed in several unrelated groups of insects, such as the Homoptera and the Raphidioidea. The fact that the wing-membrane is glassy in both the Protohymenoptera and the Hymenoptera is therefore no proof whatsoever of the genetical relationship of the two orders.

Since these are the only arguments which Tillyard has been able to advance in support of his view of the evolution of the Hymenoptera, I consider that proof of that contention is utterly lacking and that Tillyard has not produced evidence to support his conclusions.

Although Tillyard concedes that the Protohymenoptera are closely related to the Megasecoptera, he maintains that the presence of the complete external ovipositor which I described in the Protohymenoptera (*Asthenohymen*) shows that this group could not be derived from the Megasecoptera, since "out of all the complete Megasecoptera already known, there is not a single one in which an ovipositor is present." The implication of this statement is, of course, that a great many complete specimens of Megasecoptera (aside from Protohymenoptera) are known. Let us examine the facts. At the present

⁴ As a matter of fact, I had previously suggested both of the possibilities mentioned by Tillyard (*Psyche*, 1930, 37: 371).

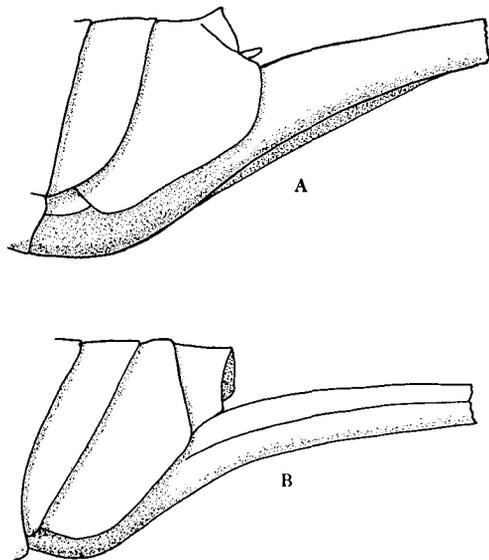


FIGURE 4. A. *Xyela* sp. (Recent, Hymenoptera), drawing of portion of ovipositor. B. *Agulla unicolor* Carp. (Recent, Raphidioidea), drawing of portion of ovipositor.

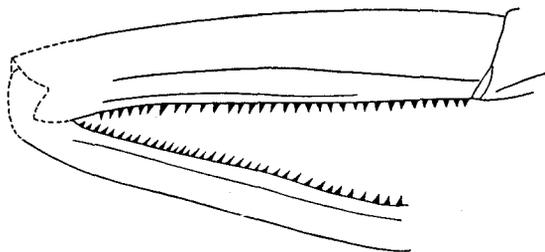


FIGURE 5. *Protodonata* sp., drawing of leg; specimen No. 4026ab, Museum of Comparative Zoölogy. Length, 48 mm.

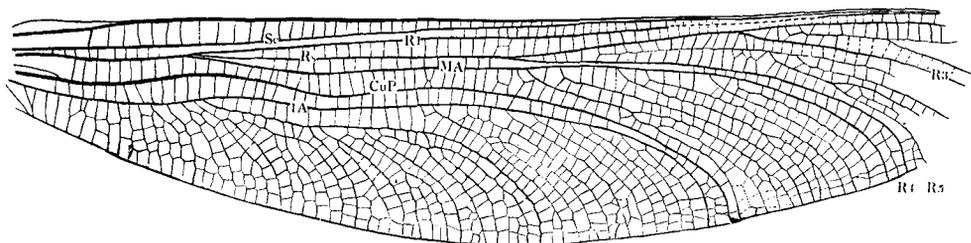


FIGURE 6. *Typus permianus* Sell., drawing of fore wing, No. 4021ab, Museum of Comparative Zoölogy.

time sixty species of Eumegaseoptera have been described.⁵ These species are based upon a total of seventy-six specimens, which of course means that three quarters of the species, at least, are represented by unique specimens. An examination of the descriptions of these fossils reveals the fact that only twenty specimens at most show any signs at all of body structure. This, then, is the series to which Tillyard referred in his phrase, "all the complete Megaseoptera known." Now let us compare this number with that of the Protohymenoptera which have been described from the Elmo limestone alone. Including those mentioned in this paper, 143 specimens are contained in the Museum of Comparative Zoölogy. If we add to this the twenty-five in the Yale collection, then we have a total of 168

⁵ The suborder Eumegaseoptera includes the typical Megaseoptera, *i.e.*, those not belonging to the suborder Protohymenoptera.

specimens of Protohymenoptera known from the Elmo limestone. Of this series a few more than forty specimens show parts of the body structure. In other words, more than twice as many Protohymenoptera as Eumegaseoptera have been studied, and twice as many of the Protohymenoptera as Eumegaseoptera have parts of the body preserved. Furthermore, the 168 Protohymenoptera have been derived from one formation and belong to only seven species; whereas the seventy-six Eumegaseoptera have been taken in several formations and belong to sixty species. It is not at all surprising therefore that we know more about the body structure of the Protohymenoptera than we do about that of the Eumegaseoptera. The tarsal segmentation, for example, is not satisfactorily known in any of the Eumegaseoptera, whereas the complete tarsi of all three pairs of legs are clearly preserved in several of the Protohymenoptera. Are we therefore justified

in concluding that, since no ovipositor has been found so far in the Eumegasecoptera, these insects lacked an ovipositor?

There are two other factors that bear on this same question. In the first place the Elmo limestone, in which most of the known Protohymenoptera have been found, is nearly white and is very fine-grained, and therefore gives much better preservation of details than is possible in the black and relatively coarse-grained Carboniferous shales, in which nearly all of the Eumegasecoptera have been collected. In the second place, the ovipositor is discernible, as such, in the Protohymenoptera only when the specimen is preserved in a lateral view. This is because the ovipositor projects only a very short distance beyond the end of the abdomen.⁶ But so far as I have been able to determine from the descriptions, not one specimen of Eumegasecoptera has been found preserved in such a way as to show a lateral aspect of the abdomen.

In view of all these facts it is my opinion that there is no justification for Tillyard's assumption that the Eumegasecoptera did not possess an ovipositor, not for his exclusion of the Protohymenoptera from the order Megasecoptera on that assumption. On the contrary, it seems very probable that an ovipositor will turn out to have existed in the Eumegasecoptera when properly preserved specimens are found. As a matter of fact, however, the absence of an ovipositor in the Eumegasecoptera would not itself exclude the Protohymenoptera from the order Megasecoptera, for it may have been present in the common ancestor of the two groups (which Tillyard admits must have been true), and yet have been lost in one subsequent line of evolution (Eumegasecoptera). In such a case there would be no more justification for separating the Protohymenoptera and Eumegasecoptera into distinct orders, than there is for similarly separating the Dilardae, which have a complete ovipositor, from the rest of the Neuroptera, which lack an ovipositor.

Order PROTODONATA

The Protodonata collected in 1935 are unusually interesting. Since some of them have a direct bearing on the classification of the proto-

⁶ It is true that the ovipositor is visible in one specimen of *Asthenohymen* preserved in dorsal view, as described in the foregoing pages; but the piece of the ovipositor is only 1 mm. long and its nature would not be obvious without the aid of a lateral specimen.

donate families, a discussion of this subject and of the evolution of the order is included after the actual description of the new specimens.

One specimen (No. 4026ab, upper layer) consisting only of the femur and tibia (figure 5) I consider to belong here because it is much too large to be referable to any other order which has been recognized in the Elmo limestone. It shows the armature of the protodonate leg better than any other fossils which have been found. The femur is 25 mm. long and the tibia, 23 mm. The inner surface of both segments is provided with heavy teeth, so closely arranged that the margins of the legs appear serrate. The tibia unquestionably has a double row of these teeth, for by chipping away its three distal teeth I exposed another series further down in the matrix. The femur possesses 23 teeth in a row, and the tibia 25 teeth. These show much individual variation in size, but this may be due to the fact that they do not actually arise in a straight line. It is not of course possible to determine even the generic position of the insect from which this leg was derived. The femur of the Carboniferous *Meganeura* was about one-sixth of the length of the wing, so that if the present specimen had wings of the same proportionate size, they must have been about 150 mm. long. This is much larger than the wing of *Typus permianus*, but is almost exactly the length of that of *T. readi* Carp.

The other Protodonata are as follows:

Family MEGANEURIDAE

Subfamily TYPINAE

The subfamily Typinae is represented in the Elmo limestone by three genera: *Typus* Sellards, *Megatypus* Tillyard, and *Oligotypus* Carpenter. The latter genus differs widely from the others by having a more poorly developed MA and a much more extensive Rs. The distinction between *Typus* and *Megatypus* is not so marked. The strongly formed "anal crossing" is probably the chief criterion of *Megatypus*. Tillyard considered the length of Sc a generic difference also, but as I have already pointed out Sc in *readi* is long, as in *Megatypus*, although the "anal crossing" is absent. The point of origin of MA, also given by Tillyard as a generic characteristic, is apparently subject to some variation in the Typinae. In my opinion, therefore, the distinctive "anal crossing" and the two rows of cellules between 1A and 2A, are the only features which serve to distinguish *Megatypus* from *Typus* satisfactorily.

Typus permianus Sell.

Figure 6

Typus permianus Sellards, 1905, Amer. Journ. Sci., (4) 22: 249-258.

Typus permianus Tillyard, 1925, *ibid.*, 10: 49.

Typus permianus Carpenter, 1931, *ibid.*, (5) 21: 104.

Megatypus vetustus Carpenter, 1933, Proc. Amer. Acad. Arts Sciences, 68: 416.

Two of the 1935 specimens belong to *Typus permianus*, one (No. 4021ab, upper layer) consisting of a very nearly complete fore wing, and the other (No. 4023ab, upper layer) of the proximal two-thirds of a hind wing. A study of these fossils, which are the most nearly complete wings of this species found since the type specimen, shows that some confusion has existed regarding the venation of *permianus*, at least in my own mind, and I have found it necessary to restudy all the specimens of this species which are in the Harvard collection. The species was originally described from a single specimen, consisting of a more or less complete insect, with the four wings out-stretched (see photograph, Carpenter, 1931, p. 105). Unfortunately, the right hind wing was the only wing completely and clearly preserved, all the others either lacking the distal third or having it poorly preserved. Eleven years ago (1927) in Austin, Texas, I examined and photographed this type specimen. I also started several drawings of parts of the wings, but at that time Dr. Sellards kindly consented to loan his entire collection to me for study purposes at the Bussey Institution, and I postponed the completion of these figures. Only a few months later, however, before the collection could be packed for shipment, all the type specimens were either lost or destroyed. The drawing of the fore wing of *permianus* which was used in my 1931 account of the Kansas Permian Protodonata was therefore based mainly on the photograph of the type and the incomplete drawings. From my examination of the newly acquired fore wing of *permianus*, I am convinced that this 1931 drawing does not depict with entire accuracy the venation of this species. In the first place, there should be a sector between R3 and R4 + 5. I am at a loss to explain why this sector was not included in my previous drawing, for although it was not clearly preserved in the fore wings of the type, it was distinct in the right hind wing and was drawn by Sellards. In the second place there should be fewer cellules between 1A and the hind margin at

the base of the wing than are shown in my 1931 figure, this part of the wing also being more nearly correctly drawn by Sellards. In the accompanying figure I have included a drawing of the new fossil which is almost a complete wing (No. 4021). A comparison of this with the descriptions and figures given by Sellards leaves no doubt that it is *permianus*.

With the venation of *permianus* clarified, it is obvious that *Megatypus vetustus*, which I described from a distal third of a wing in 1933, is *Typus permianus*. A slight individual variation in the position of origin of R4 + 5 is undoubtedly sufficient to explain my error in assigning this specimen to *Megatypus*; and once in *Typus*, it is clearly *permianus*.

The restudy of the venation of *permianus* leading to the conclusion that Sellards' figures of *permianus* were more nearly correct than either Tillyard or I had supposed, raises the question of the presence of the subnodus and the so-called oblique vein ("O") which Sellards described between the base of "M2" (R3) and "Rs" (sector) below it. My intention to examine Sellards' type for these structures was of course frustrated by the loss of the specimen before it was sent to me. Tillyard had examined a photograph of the type sent to him by Sellards, and, seeing no sign of the oblique vein, was apparently led to the conclusion that it was not present. He implies the same about the subnodus. I have seen no specimens with the latter preserved, but it should be noted that in all the specimens of *permianus* in the Harvard collection showing this area of the wing, the part where the subnodus would be located is broken away.⁷ So far as Sellards' oblique vein ("O") is concerned, it is true that such a vein does occur in some specimens of *permianus*, but the slope of the vein is subject to much variation and at times the vein is practically perpendicular to the lower vein it joins.

Typus readi Carp.

Figure 7

Typus readi Carpenter, 1933, Proc. Amer. Acad. Arts Sci., 68: 415, fig. 1.

⁷ The unnamed fragment of a Protodonatan, figured in part 6 of this series (p. 417), has a short vein present in the position of Sellards' subnodus, but several odonatologists and other entomologists have expressed the opinion to me that the peculiar structure of this wing was probably the result of an injury to the nymphal wing pad.

This species was originally based upon a well preserved hind wing, lacking the proximal and distal parts. In the 1935 collection there is a specimen of a wing (No. 4022ab, upper layer), which I consider to be a fore wing of this species. That it is a fore wing is clearly shown by the relatively narrow anal region, and the more gradually undulated CuP and 1A. This wing possesses the two chief characteristics of *readi*: (1) the subcosta does not terminate until at least almost the apex of the wing, so that in the region above the point of separation of R2 and R3 it is much further from the costa than it is in *permianus*; (2) R4 + 5 arises at a point well proximad of the origin of the first branch of MA. The new specimen is 100 mm. long and 30 mm. wide, which indicates that the whole wing was almost exactly the size of the holotype. The similarity of the venation of the two wings is very striking, the origin of even the⁸ minor veins being almost identical in position. The fore wing (No. 4022ab) is 105 mm. long and has a maximum diameter of 30 mm. Unfortunately, as in the type, the area just above the forking of R2 + 3 is partially broken away in the fore wing, so that we are unable to determine whether or not the structure of this part of the venation is like that described by Sellards in *permianus*.

In all probability the specimen (No. 5009, Peabody Museum) which Tillyard figured and described as the fore wing of *Megatypus schucherti* (1925, p. 57, fig. 8) belongs to *readi*. Tillyard stated in his account of this poorly preserved fragment that its venation differed from that of the hind wing (previously described) "only" in the much narrower anal area; but, as shown in his figure, the most significant difference is that in the fragment of the fore wing, R4 + 5⁹ arises far proximad of the origin of the first branch of MA, and not far distad of the origin of the latter, which was true of the hind wing, and which Tillyard selected as one of the characteristics of the genus *Megatypus*. This difference clearly indicates that the two specimens do not belong to the same species. Since the early origin of Rs is the chief characteristic of *Typus readi*, it is very probable

that the fragment of the fore wing belongs to *readi*.¹⁰

Megatypus ingentissimus Till.

Megatypus ingentissimus Tillyard, 1925, Amer. Journ. Sci., (5) 10: 58, fig. 9.

In his account of the small fragment on which this species was based Tillyard attempted to estimate the size of the complete wing by comparing the distances between the apex and the end of R4 + 5 (R3 of Tillyard's figure) in this fossil and in *Typus permianus*. He concluded that the complete wing must have measured over 250 mm., which is only a little short of the size of *Meganeura*. Unfortunately, there seems to have been an error in Tillyard's computation. The distance from the end of R4 + 5 to the apex of the wing in *T. permianus* is one-fifth of the entire length of the wing. In the specimen of *M. ingentissimus* this same distance is 24 mm., which would indicate that the total wing length was not over 125 mm., about half the dimension estimated by Tillyard. This is consistent with the size of the veins and cells as actually preserved in the fragment. The question of the size of *ingentissimus* arose in my mind in connection with the identification of *Meganeuropsis permiana*, described in this paper.

It should be noted also that there is really no evidence indicating that this species belongs to *Megatypus*, since the long Sc, as I have mentioned above, is also present in *Typus*.

Subfamily MEGANEURINAE

Meganeuropsis, new genus

Allied to *Meganeura*, but differing in having the proximal part of the costa curved, and the proximal portions of CuP and 1A almost straight.

Meganeuropsis permiana, n. sp.

Figure 8

This species is based upon two fragments of a wing: one (No. 4024) consists of the proximal

¹⁰ Following his description of the two specimens of *schucherti*, Tillyard designated both of them as holotypes (p. 58),—one as the holotype hind wing, the other as the holotype fore wing. However, not by any accepted definition of a holotype is it possible to have two holotype specimens of one species; even the obverse and reverse of a holotype specimen are only counterparts of the one type. The true holotype of *schucherti* is the specimen of the hind wing (No. 1021ab), since that was described and designated as the holotype first. The fragment of the fore wing is of course only a paratype.

⁸ Further cleaning of the type specimen of *readi* (No. 3253ab) reveals a sector between R2 and R3, at the very apex of the fossil, which was not included in my original figures of *readi*.

⁹ In this descriptions and discussions of *Megatypus* Tillyard designated R4 + 5 as R3, but he corrected this error in a later paper (1928, p. 161).

region, from the base to a point well beyond the origin of R4 + 5; the other (No. 4025) consists of the area between R4 + 5 and 1A, in the region of the first branch of MA. Both of these fossils were collected by the writer and were undoubtedly parts of one individual insect. The proximal piece was found first about a half inch below the top of the upper layer of the limestone. Unfortunately, the latter was already broken up into irregular pieces by underground weathering (see plate 1, fig. 1) so that an attempt to follow the wing along at the same level in the limestone was only partially successful. The second portion of a wing was found at exactly the same level in a block of the limestone less than two feet away from the place where the first fragment was secured. Since no other specimen of this species or genus has been found in the limestone, I am convinced, as stated above, that the two fragments are part of the same individual. In order to determine the relationship between the fragments, drawings of each were made to the same scale, that of the second piece being made on tracing paper. It was found that the two fragments fitted together very readily but also that there was slight overlapping of the areas included. The fragments are therefore not portions of the same wing.

The proximal fragment (No. 4024, figure 8A) is 140 mm. in length, from the base of R + M to the broken end of MA. This piece of the wing having been covered by and infiltrated with calcite, only a few of the cross-veins are discernible, but it is not difficult to determine the structure of the main veins. Only the proximal piece of the precostal space is evident; the width of this, however, indicates that the rest of the area was about the same as that in *Meganeura*. The costa is close to the subcosta at the base, but soon curves anteriorly. R is distinctly independent from the stem of M, as in *Meganeura*, and diverges away from MA at a point just above the highest crest of CuP. Rs apparently arises at this separation, but its exact origin is not discernible. Although the area between Rs and MA is very poorly preserved, it is possible to distinguish clearly R4 + 5; the precise origin of this vein cannot be determined, but it is obviously located not far from the origin of Rs, this being the chief characteristic of the subfamily Meganurinae. In all probability these two veins separate at a narrow fork instead of by an abrupt divergence of one of them.¹¹ CuP and 1A are

formed as in *Meganeura* except that their proximal parts are nearly straight. The true margin of the wing is not visible anywhere in this specimen, and it is impossible to determine how broad the wing actually was; but in view of the shape of the wings of *Meganeura*, it was probably half again as wide as the preserved portion. The few cross-veins that are preserved indicate an arrangement similar to that of *Meganeura*. In the area between CuP and 1A there is a single oblique cross-vein, similar to the one or two present in *Typus*. Although this fragment (No. 4024ab) of the wing is not so well preserved as the more distal piece, it includes the important taxonomic characters and is therefore designated as the holotype of the species.

The second piece (No. 4025ab, paratype) of this species is perfectly preserved. The first branch of MA arises at the same point, with respect to the curvature of CuP, as it does in *Meganeura*, and it forms a distinct fork, as in the latter. 1A gives rise to a series of straight veinlets, as is characteristic of the subfamily Meganurinae.

When these two fragments are fitted together, it becomes apparent that in spite of the perfect correspondence in other details, the distance between R4 + 5 and MA is greater in the second (distal) piece than in the first; and it is also clear that R4 + 5 is straight, not curved upward to meet R2 + 3, as seems to be the case in the proximal fragment. In this respect, R4 + 5 of the second piece is formed exactly as it is drawn by Brongniart in *Meganeura monyi* (1893, plate 25). The most likely explanation of these differences is that one fragment is part of a hind wing and another part of a fore wing, and this view is substantiated by the fact that the various wing fragments of *Meganeura* show a similar difference of structure. Unfortunately, not enough well preserved specimens of *Meganeura* have been found to indicate which is the fore or hind wing.

Like *M. monyi*, *Meganeuropsis permiana* was a

confusion has existed in the literature regarding the origin of Rs and R4 + 5 in *Meganeura*. Lameere (1917) has pointed out that Brongniart's original restoration (1892) on plate 25 is correct, although the drawings of the actual fossils on the preceding plate are inaccurate. The restorations by Handlirsch (1908, 1920) and Tillyard (1917) followed the latter drawings and are consequently incorrect. In another paper (1919) by Handlirsch, the reconstruction of the megarid venation depicts the origins of Rs and R4 + 5 as they were originally restored by Brongniart.

¹¹ In this connection it should be noted that much

huge insect. The fore wing of *monyi*, which has been recognized as the largest insect so far discovered, was about 300 mm. (or 12 inches) in length, the entire wing expanse being about 27 inches. In order to obtain an estimation of the size of *M. permiana*, a drawing of the type specimen was made on tracing paper and placed over Brongniart's figure (natural size) of the wing of *M. monyi*. This comparison showed that the wing of *M. permiana* was slightly larger than that of *monyi*. If the wings of the former were shaped like those of *monyi*, then the wing of *permiana* must have been about 330 mm. (or about 13 inches) long, indicating a wing expanse of approximately 29 inches (710 mm.). Because of the fragmentary condition of the specimens of *Meganeuropsis permiana*, it is difficult to indicate differences between *Meganeuropsis* and *Meganeura*; but I have considered it preferable to erect a new genus for this species, rather than to place it in *Meganeura*, thus extending the range of that genus to the Permian and to the New World.

The occurrence of *M. permiana* in the Elmo limestone furnishes another illustration of the diversity of structure among the insects of this Permian deposit. In the same fauna there existed such minute insects as the Psocopteron *Cyphoneura permiana* Carp., with a wing expanse of less than 3/8 of an inch (4 mm.). No other known insect fauna, Recent or fossil, exhibits such diversity in size.

THE CLASSIFICATION AND EVOLUTION OF THE PROTODONATA

During the past ten years the classification of the Protodonata has been discussed and modified by several students of fossil insects. Handlirsch in his catalogue of Palaeozoic insects (1922) recognized four families in this order: Paralagidae, Meganeuridae, Protagriidae, and Typidae. Following the publication of Lameere's theory of wing venation in 1921, Tillyard proposed (1925) that the order be divided into two families: Protagriidae, including those species in which MP and CuA were fully developed; and Meganeuridae, in which MP and CuA were absent or possibly reduced to mere vestiges at the base of the wing. The latter family he divided into three subfamilies, Paralaginae, Meganeurinae, and Typinae. This classification was used in my 1931 account of the Kansan Protodonata, though I stated that in my opinion the characteristics separating the families Protagriidae and Meganeuridae were of subordinal rather than family

rank. A similar treatment of the families was independently advocated by Martynov (1932), who proposed further separation of the family Meganeuridae by establishing for it a new order, Meganisoptera. At the same time he erected a new family (Calvertiellidae) for the genus *Calvertiella* from the Kansan Permian, and following Lameere transferred the family Cockerelliellidae from the Palaeodictyoptera to the Protodonata. Martynov therefore considers the order Protodonata to consist of three families: Protagriidae, Calvertiellidae, and Cockerelliellidae. Later in 1932 Martynov was led to conclude that the insects comprising the order Meganisoptera were not sufficiently different from the true Odonata to justify their exclusion from that order, and therefore placed the family Meganeuridae, with its subfamilies, in the Odonata. Tillyard, in his latest and last discussion of the subject, accepts Martynov's proposal of isolating the Meganeuridae from the Protodonata, but also favors their exclusion from the Odonata because of their lack of a true nodus.

In my opinion there is no justification for isolating the Meganeuridae from the rest of the families formerly included in the Protodonata, until it has been proven that the Meganeuridae have had a phylogenetic origin different from that of the other families. At the present time there seem to be no facts to support such a conclusion. It is also my opinion that the Meganeuridae should be excluded from the true Odonata until evidence has been secured showing that the Meganeuridae are in the phylogenetic line leading directly to the Odonata or that they have been derived from the *immediate* ancestor of the Odonata. There are undoubtedly many points of similarities between the Meganeuridae and the Odonata, but these I believe to be characteristics which were present in the remote common ancestors of the two groups, or which have appeared in the Meganeuridae and Odonata as a result of parallel evolution. The more important of the similarities between the members of these two categories, as indicated by a comparison of the Protanisoptera with the Meganeuridae, are the absence of MP and CuA, the distinctive origins of Rs and MA, the presence of the supposed remnant of CuA at the base of the wing, and the undulation of CuP. All of these characteristics, I believe, were possessed by the common ancestor of the Meganeuridae and the Odonata. My reasons for this conclusion will be given below.

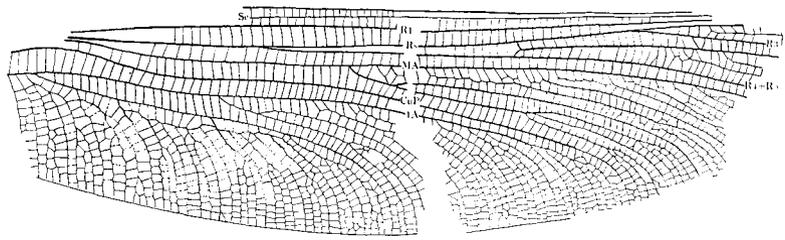


FIGURE 7. *Typus readi* Carp., drawing of fore wing; No. 4022ab, Museum of Comparative Zoölogy.

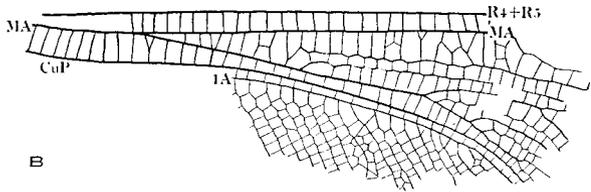
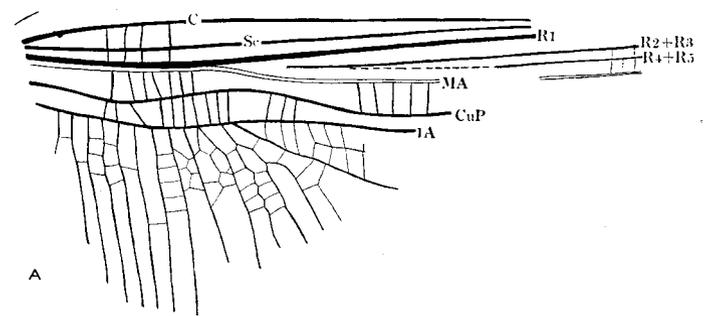


FIGURE 8. *Meganeuropsis permiana*, n. sp., drawings of venation. A, holotype, No. 4024ab; B, paratype, No. 4025ab, Museum of Comparative Zoölogy.

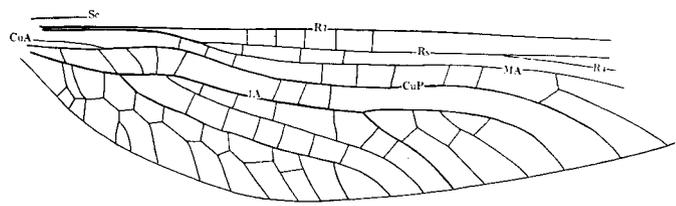


FIGURE 9. *Erasipteron larischi* Pruvost, drawn from photograph. Carboniferous, Czechoslovakia.

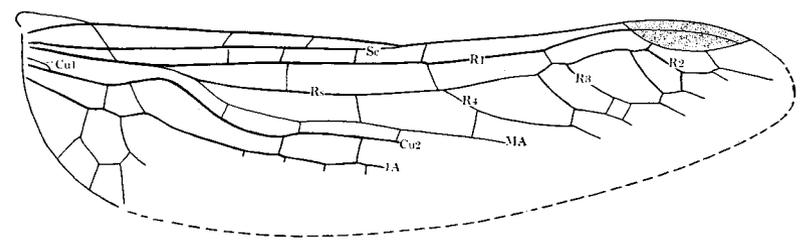


FIGURE 10. *Ditaxineura anomalostigma* Till., drawing of hind wing; specimen No. 3972ab, Museum of Comparative Zoölogy.

The absence of the nodus from the Meganeuridae, although removing them from the true Odonata, does not necessarily eliminate them from the phylogenetic line leading to the Odonata. But the most striking difference between the Meganeuridae and the most generalized Odonata (whether termed Protanisoptera, Permanisoptera, or Permodonata) is in the number of cells in the wings. In the fore wing of *Typus permianus*, for example, which is typical of the Meganeuridae so far as the number of cross-veins is concerned, there are upwards of a thousand cells. In the Protanisoptera, however, there are at the most two hundred (*Polytaxineura*, *Permaeschna*, *Pholoptilon*), with less than 100 in *Ditaxineura*, the oldest and most generalized of the anisopterous Odonata. It seems apparent to me that the network of cellules in the Meganeuridae is a specialization not to be expected in the ancestor of the Odonata. For this reason, following a study of the Permian Odonata in 1931, I was led to the conclusion that the families of Protodonata known to us were really highly specialized members of the order, and that the "earliest and most primitive representatives were much more like the forms which we postulate as ancestors of the true Odonata."

Much support has been given to this view by the subsequent discovery of the protodonatan, *Erasipteron larischi* Pruvost (1934), from the Upper Carboniferous (Upper Namurian) of Czechoslovakia. The importance of this fossil lies in the fact that it is geologically *the oldest known member of the order*. A drawing of the specimen, made from a photograph kindly sent to me by Dr. Pruvost, is included here (figure 9). This fossil consists of a well preserved wing, probably a fore wing, which lacks the anterior margin and the apical region. The most striking feature of the wing is the relatively small number of cross-veins. On the basis of the structure of the preserved part of the wing, it is probable that the complete wing included less than a hundred cells, about the same number as is present in *Ditaxineura*. In addition the wing of *Erasipteron* has also all of the odonate characteristics previously mentioned which are common to the Meganeuridae and the Protanisoptera—the absence of MP and CuA, the distinctive origin of Rs and M, the undulation of CuP, and the supposed remnant of CuA. The loss of a complete MP and the presence of the supposed remnant of CuA are especially interesting, since they show that the reduction of MP and CuA

occurred as far back as the lower part of the Upper Carboniferous, before the deposition of the Comenry shales. It is unfortunate that the nodal region of the *Erasipteron* wing is not preserved; in all probability an incipient nodus was present. In my opinion the ancestors of the true Odonata were very much like *Erasipteron* (though it is improbable that *Erasipteron* itself was in the direct line of that ancestry), rather than like *Meganeura* or any of the other Meganeuridae. Pruvost assigned *Erasipteron* to the family Paralagidae, which has previously been known only from the Carboniferous of North America. The distinctive feature of the Paralagidae is the very short subcosta, which is not preserved in the type of *Erasipteron*. The wings of the Paralagidae, however, are as closely netted with cellules as those of the Meganeuridae. With its small number of cells the genus *Erasipteron* is unique among all the Protodonata and it unquestionably requires the erection of a separate family, **Erasipteridae** (new family) for its reception. The position of this family in the Protodonata is apparent from the following table which summarizes my present conception of the classification of the families of the order:¹²

Suborder **Euprotodonata**, new suborder (MP and CuA present).

1. Family Protagriidae, Handl. Upper Carboniferous of Europe.
2. Family Calvertiellidae Mart. Permian of Kansas.

Suborder Meganisoptera Mart. (MP absent, CuA absent or possibly vestigial).

1. Family Erasipteridae, new family. Upper Carboniferous of Europe.
2. Family Paralagidae Handl. Upper Carboniferous of North America.
3. Family Meganeuridae Handl. Upper Carboniferous of Europe, Permian of Kansas, Arizona, Russia.
 - A. Subfamily Meganeurinae Handl. Upper Carboniferous of Europe, Permian of Kansas.
 - B. Subfamily Typinae Handl. Permian of Kansas, Arizona, Russia.

In this table I have regarded the Meganeurinae and Typinae as separate subfamilies rather than as families, as they have been treated by Handlirsch. It is true that there are more differences between the members of these two subfamilies

¹² The family Cockerelliellidae is omitted from this list, since I consider it to be a Palaeodictyopteron, rather than a Protodonatan.

than have previously been recognized. Tillyard stated (1928, p. 162) that the Typinae differ from the Meganeurinae "only" in having R4 + 5 arise far distad of the origin of MA; but in addition to this there are also other differences: the precostal space, which is limited to the very base of the wing in the Typinae, extends to the middle of the wing in the Meganeurinae; the first branch of MA arises at the middle of the wing in the Typinae, but in the proximal half of the wing in the Meganeurinae; and the branches extending from the sectors of 1A to the hind margin are curved in the Typinae but are almost straight in the Meganeurinae. These differences, however, seem hardly sufficient to justify separation of the groups by family ranking.

Until the present time the subfamily Meganeurinae has been found only in the Upper Carboniferous of Europe. The occurrence of *Meganeuropsis*, which is unquestionably a true meganeurine, in the limestone is therefore of much interest. This fossil not only extends the geological range of the Meganeurinae into the Permian, but extends likewise its geographical range into the New World.

Order ODONATA

True Odonata are among the rarest of the insects occurring in the Elmo limestone. Up to the time when the 1935 collection was secured, only 13 specimens were contained in the combined Sellards (1), Yale (4) and Harvard (8) collections. In the new material there are 7 more specimens, which bring the total to 20 and add in many respects to our knowledge of the structure of these earliest Odonata.

Suborder Protanisoptera

Family DITAXINEURIDAE

Ditaxineura anomalostigma Till.

Figure 10

Ditaxineura anomalostigma Tillyard 1926, Amer. Journ. Sci., (5) 11: 71-73.

Ditaxineura anomalostigma Carpenter, 1931, *ibid.*, (5) 21: 123-124.

Two specimens of this insect were found in 1935, both in the upper layer. One of these (No. 4027) consists of the distal half of a fore wing, and deserves no further comment. The other (No. 3972) is an incomplete hind wing, which, although lacking part of the posterior area, contains those portions of the venation of greatest phylo-

genetic interest. This fossil is therefore a most important one, since it is the first specimen of a protanisopterous hind wing which has been found (with the exception of a very minute fragment, figured by Tillyard in 1935, from the Upper Permian of Australia). This hind wing is 19 mm. long, a little shorter than the fore wing (21 mm.), which I have previously described in detail (1931).¹³ The width at the proximal part of the wing (the only part of the fossil which includes the posterior margin) is 4.6 mm. This is somewhat greater than the width of the same part of the fore wing, which measures 2 mm. The maximum width of the fore wing, at about the middle line of the wing, is 5 mm., and it is probable that the maximum width of the hind wing was not much greater than the proximal width. The precostal area of the hind wing is similar to that of the fore, and R1, Rs, and the pterostigma are essentially the same as in the fore. Sc, however, terminates almost exactly at the middle of the wing, which is more proximad than in the fore wing. This difference between the fore and hind wings is one that is also found in the existing Anisoptera. The region of the arculus is of course especially interesting. As in the fore wing, M is coalesced proximally with Rs, but Rs + M diverges from R much more abruptly than it does in the fore wing; this is also true of the separation of M from Rs. The result of these abrupt divergences is to produce a condition which is a definite approach to the structure of the arculus in the Jurassic *Tarsophlebia* (Anisozygoptera). The small vein at the base of the wing, designated as Cu1, is well developed. Cu2 is strongly undulated, much more so than it is in the fore wing, but this is not true of 1A; as a result of the form of these two veins, the space between them is greater than in the fore wing. The area between 1A and the posterior margin is considerably wider than in the fore wing; in this area there has been an increase in the number of rows of cells.

From the foregoing account it is apparent that the hind wing of *D. anomalostigma* differs from the fore wing chiefly in four respects: (1) the broader anal area; (2) the shorter Sc (more proximal nodus); (3) more abrupt divergence of Rs and M at their origins; and (4) greater curvature of Cu2. The significance of these differences is that they are the same as those which exist between the fore and hind wings of the Recent

¹³ As a result of a misprint, the length of this wing was published as "2.1" mm., instead of "21" mm. (1931, p. 123).

Anisoptera and the extinct Anisozygoptera. Such a condition is in perfect agreement with the view that the Protanisoptera were ancestral to the true Anisoptera.

Since my previous discussion of the Protanisoptera was written (1935) Tillyard has described from the Upper Permian of Australia (1935) another genus, *Polytaxineura*, which belongs to this suborder. In view of the similarity between *Polytaxineura* and *Pholidoptilon* Zalessky (from the Upper Permian of Russia), Tillyard placed these genera in one family. This family he termed Polytaxineuridae, stating that Zalessky did not propose a family name for *Pholidoptilon*. Unfortunately he seems to have overlooked Zalessky's use of the name Pholidoptilidae for the family to include his genus; this name was actually proposed by Zalessky with his description of the genus (1931a, 1931b) and of course has priority over the name Polytaxineuridae.

Suborder Protozygoptera

Family KENNEDYIDAE

Kennedy mirabilis Tillyard

Figure 11

Kennedy mirabilis Tillyard, 1925, Amer. Journ. Sci., (5) 10: 66-72.

Kennedy mirabilis Carpenter, 1933, Proc. Amer. Acad. Arts Sci., 68: 418.

One specimen of this rare insect (No. 3971ab, upper layer) was found in 1935; it is the first complete wing of the species and genus which has been secured. The venation is almost identical with that of the type specimens, and the differences that do exist, such as in arrangement of the cross-veins at the end of M, are hardly more than individual variations.¹⁴ The wing has a length of 25 mm., and a maximum width of 3.3 mm. It is accordingly very much smaller than the type, which is 44 mm. long and 5.8 mm. wide. Although this is a decidedly greater variation in size than usually occurs in Odonata (a ratio of .56), Professor Calvert has called my attention to a record of an even greater variation in a Recent Zygopteron, *Megaloprepus caerulatus* (Drury) (Calvert, 1923).¹⁵ Regardless of the

¹⁴ It should be noted that in Tillyard's figure of *mirabilis* (1925, fig. 10) the veinlets between Cu2 and the posterior margin are not correctly drawn; they should be somewhat oblique and sigmoidal, as shown in his photograph (figure 12B).

¹⁵ I am indebted to Professors C. H. Kennedy and

striking difference in the wing length between the type and the present specimen, therefore, I regard them as belonging to the same species.

A second specimen of *Kennedy* (No. 3974ab) may also belong to *mirabilis*; it consists of the distal half of a poorly preserved wing.

Kennedy tillyardi, n. sp.

Figure 12

Fore wing: Length 33 mm., maximum width, 4 mm. Petiole longer and more slender than that of *mirabilis*; two antenodals, more widely separated than in *mirabilis*; 4 postnodals; pterostigma about twice as long as in *mirabilis*; Rs and MA arising as in the latter, but MA with a prominent upward curve a short distance beyond its origin; R4 + 5 arising at about the middle of the wing; branches of Rs as in *mirabilis*, except that at least one cross-vein is present between 1R2 and R2; stem Cu2 + 1A slightly more curved than in *mirabilis*; fork of Cu2 and 1A narrow, Cu2 at this point being very close to the origin of MA; m-cu cross-vein very oblique, almost parallel with the longitudinal axis of the wing; 1A much closer to the hind margin than in *mirabilis*.

Holotype: No. 3970ab, Museum of Comparative Zoology; collected by F. M. Carpenter in the upper layer of the Elmo limestone. The specimen consists of a fore wing, complete except for a slight tear in the posterior margin near the apex. The species is named for the late Dr. R. J. Tillyard.

Although this wing is similar to that of *mirabilis* in general features, the longer petiole and stigma, and the position of 1A show beyond doubt that it represents a distinct species.

Kennedy reducta, n. sp.

Figure 13

Based upon the distal third of a wing. Length of fragment 11 mm.; width 3.6 mm.; pterostigma short, as in *mirabilis*, R2 + 3 remote from R1; 1R2 separating from R2 below the pterostigma; no cross-veins between 1R2 and R2; R3 arising slightly proximad of the pterostigma, only one cross-vein between it and 1R2; 1R3 arising almost directly above the end of 1A, only two cross-veins between it and R3, and only three cross-veins between 1R3 and R4 + 5.

P. P. Calvert for their opinions on the significance of the difference in size of the specimens of *K. mirabilis*.

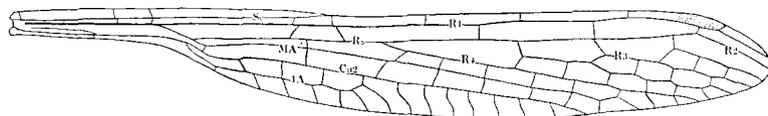


FIGURE 11. *Kennedyya mirabilis* Till., drawing of venation; specimen No. 3971ab, Museum of Comparative Zoölogy.

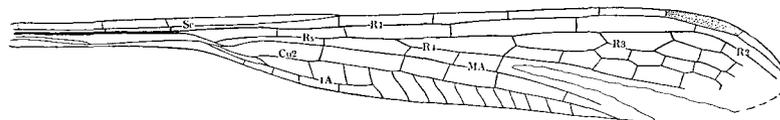


FIGURE 12. *Kennedyya tillyardi* n. sp., drawing of venation; holotype, No. 3970ab, Museum of Comparative Zoölogy.

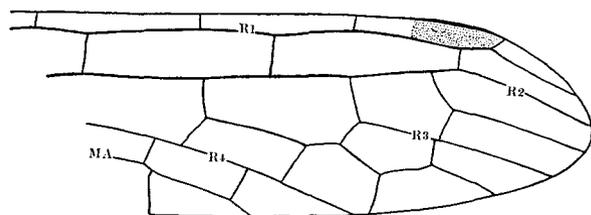


FIGURE 13. *Kennedyya reducta* n. sp., drawing of venation; holotype, No. 3973ab, Museum of Comparative Zoölogy.

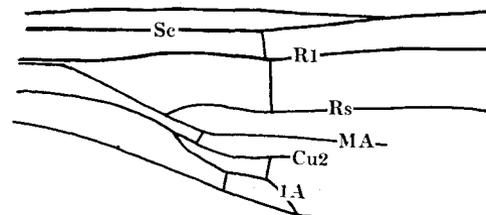


FIGURE 14. *Progoneura minuta* Carp., drawing of arcus region; specimen No. 3975, Museum of Comparative Zoölogy.

Holotype: No. 3973ab, Museum of Comparative Zoölogy, collected by F. M. Carpenter in the upper layer of the Elmo limestone in 1935. This specimen consists of a splendidly preserved distal third of a wing.

A comparison of this wing with that of *mirabilis* indicates that the complete wing was probably about 35 mm. long, nearly the same size as the type of *tillyardi*. The wing differs from that of the other species of *Kennedyia*, and of all other described Protozoptera, by the small number of cells in the region of the branches of Rs; thus, between R3 and R4 + 5 there are only 2 cells in *reducta* instead of 5 or 6, as in *mirabilis* and *tillyardi*. If the same condition prevails throughout the rest of the wing, it may eventually be found advisable to establish a distinct genus for *reducta*.

Progoncurea minuta Carp.

Figure 14

Progoncurea minuta Carpenter, 1931, Amer. Journ. Sci., (5) 21: 120.

Although only a fragment of a wing of this species was also found in 1935, this specimen (No. 3975, upper layer) is of interest because it includes the arculus region and details which are better preserved than those in the other two known specimens. My figure of this region in the type specimen (p. 117) was necessarily diagrammatic because of the poor preservation; I therefore include here a drawing of the arculus of the new specimen. The proximal cross-vein between R1 and Rs is present, as in the other species of *Kennedyidae*. The stem of Rs + MA is even longer than I had supposed it to be. The fossil shows clearly the chief characteristic which separates this genus from *Kennedyia*: the very short 1A, terminating almost directly below the arculus.

Order HOMOPTERA

Some of the most interesting insects found in 1935 are Homoptera. Twenty-six specimens were collected, all but five being derived from the upper layer of the limestone. Although no undescribed species were secured, the new lot of fossils is significant because of its contribution to our knowledge of the body structure and hind wings of these earliest Homoptera.

A study of the additional Homoptera shows that the classification of the Lower Permian species needs to be greatly modified. In 1931, in my first account of these insects, I concluded that

all the Lower Permian Homoptera which had been described were members of the family Archescytinidae, and both Tillyard and Martynov have accepted this view. In later papers (1931, 1933) I established two other families for the Lower Permian Homoptera, Cyphoneuridae (1931) and Lithoscytinidae (1933). The former was erected for two species, consisting of wings with a very reduced venation, which were closely related to the genus *Lophioneura* Till. (Permian of Australia), placed by Tillyard (1921) in the Homoptera. More recently, however, Tillyard secured several nearly complete members of this same group of insects and from his examination of them concluded (1935) that the mouth-parts were mandibulate, and that the whole series of insects belonged to the Psocoptera. As I mentioned at the time of the description of *Cyphoneura*, I suspected the possibility of the affinities of these insects with the Psocoptera on the basis of the wing venation, but believed that most of the evidence pointed to the Homoptera. Since Tillyard's conclusion seems fairly certain, we may, tentatively, at least, consider the family Cyphoneuridae as not homopterous.

The second family, Lithoscytinidae, was established to include a remarkable wing which differed from all other Homoptera by having Cu1 entirely free from the media for its entire length. Except for this striking peculiarity, this wing was like those of the Archescytinidae. Martynov had then just described (February, 1933) several archescytinids from the Upper Permian of Russia, including one hind wing which was more triangular than the fore wings and had all the characteristics that would be expected in the hind wing of the Archescytinidae. Now one of the archescytinids (*Permoscytina kansasensis*) collected in 1935 is fairly complete, including both fore and hind wings. The hind wing is not at all like the one which Martynov described as an archescytinid, for it has the free Cu1 of *Lithoscytina* (figure 17). The latter genus, therefore, was obviously founded upon the hind wing of an archescytinid. The family Lithoscytinidae consequently becomes synonymous with the Archescytinidae, which remains the only family of Homoptera so far known from the Lower Permian.

It is also necessary to make some changes in the generic classification of the Archescytinidae. The genus *Archescytina* itself was established by Tillyard for one species represented by a very well preserved wing, the outstanding characteris-

tic of which was a well developed subcosta, remote from the radius for its entire length. This venational feature was an important one since in no other Homoptera has a similar condition of Sc been known. None of the three incomplete wings of this species which were contained in the 1927 Harvard collection showed the area between the costal margin and the radius satisfactorily, and I assumed that my inability to discern the subcosta in those specimens was the result of their poor preservation. Only the reverse of the type was at that time (1931) in the Peabody Museum, the obverse still being in Dr. Tillyard's possession; consequently when I failed to find Sc in the reverse of the type, the costal area of which was not well preserved, I concluded that it was undoubtedly clear enough in the obverse. However, my suspicions about the structure of the subcosta were aroused when several specimens in the 1935 collection were found to be identical with *Archescytina* except that the subcosta was formed as in the other Permian Homoptera. Meanwhile, the obverse of the type of *Archescytina permiana* had been returned to the Peabody Museum by Dr. Tillyard, and an examination of this fossil failed to reveal any sign whatever of a free and isolated subcosta.¹⁶ A photograph of the obverse of this type is shown in plate 2, figure 1. This is more than a mere taxonomic correction, for because of the supposed free subcosta, *Archescytina* has been regarded as the most generalized of the known Homoptera, and Tillyard's figure of it has been reproduced in various publications by other students of insect phylogeny.

The removal of this supposedly distinctive feature places *Archescytina* very close to the other genera of Archescytinidae. In fact it is difficult to find generic characteristics in the wings by which to separate *Archescytina* from *Permopsylla*. The only characteristic which might be accepted as of generic value is the longer free Cu1 in the fore wing of *Archescytina*. This is a slight difference to be sure but it nevertheless seems advisable not to synonymize *Permopsylla* with *Archescytina* until the body structures have been found to be similar.

¹⁶ Tillyard states in his original description of this fossil that the course of Sc is not apparent at first, but can be seen if the lighting is properly arranged. However, even various arrangements of the illumination failed to reveal any trace of the free Sc described by Tillyard, although the other veins of the wing are preserved with striking clearness. Professor Dunbar, who examined the type specimen with me, has substantiated my conclusion.

Permopsylla is still a valid genus. The genotype, *kansasensis*, differs markedly in having R + M straight, not arched as in *Archescytina* or *Permopsylla*. This characteristic is very clearly indicated in the type of *kansasensis* (photograph, Tillyard, 1926, p. 384), and also in a new specimen contained in the 1935 collection. However, it is now necessary to make a change in the generic position of *Permopsylla muiri* Till. Tillyard remarked at the end of his original description that this insect was nearer to the genus *Archescytina* than to the genotype, *Permopsylla kansasensis*, but he placed it in *Permopsylla* because it did not have the supposedly free Sc of *Archescytina* nor the curved R + M. However, as I have previously stated (1931, p. 114) R + M actually was curved in the type of *muiri* and it is now also apparent that *Archescytina* did not possess a free Sc. Obviously, then, *muiri* belongs to *Archescytina*, differing from the genotype (*permiana*) only by its size.

At present, therefore, there seem to be only four genera of Homoptera in the Elmo limestone, and these are separated mainly on the characteristics indicated in the following key:

1. R + M straight *Permopsylla* Till.
R + M arched 2.
2. Free proximal piece of Cu1 much more than half as long as R + M *Archescytina* Till.
Free proximal piece of Cu1 at most only half as long as R + M 3.
3. Cu1 forked *Permopsylla* Till.
Cu1 unbranched *Paleoscytina* Carp.

With the following account of the Homoptera collected in 1935 I have included redescrptions of all the above genera except *Paleoscytina*, in order to clarify the generic characteristics.

Family ARCHESCYTINIDAE

Genus *Archescytina* Tillyard

Archescytina Tillyard, 1926, Amer. Journ. Sci., 11: 385.

Tegmen: anterior margin straight or slightly concave, never convex; Sc close to R and R1 and weakly developed; R + M arched towards the anterior margin; Cu contiguous with M at the very base of the wing; free proximal part of Cu1 arched towards the posterior margin of the wing, joining M before it separates from R; Cu1 forked distally; two cross-veins, one (r-m) between M and Rs; the other (m-cu) between Cu1 and M3 + 4.

Hind wing: very similar to the fore wing in shape and venation, except that the stem R + M is a little shorter, Cu1 is free from M for its entire length, and 2A is much reduced.

Body structure (known only in *A. permiana*): antennae slender, filiform, containing about 25 segments; beak well developed; tarsi three-segmented.

Genotype: *Archescytina permiana* Till.

Archescytina permiana Till.

Figure 15; plate 2, figure 1

Archescytina permiana Tillyard, 1926, Amer. Journ. Sci., (5) 11: 386; fig. 4.

Archescytina permiana Carpenter, 1931, Amer. Journ. Sci., (5) 22: 115; fig. 1.

Tegmen: length 8–8.5 mm.; width, 2.5–3.0 mm. Rs arising either half way between the origin of M and the fork of R1 (type) or slightly nearer to the latter; cell between Cu1a and Cu1b somewhat variable in shape, but always very large; Cu2 terminating at a point nearer to 1A than to Cu1b; 1A slightly curved sigmoidally.

Hind wing: length, 7 mm., width, 2.5 mm.; anterior margin shaped as in the fore wing; cell between Cu1a and Cu1b slightly narrower than in the fore wing; 1A sigmoidally curved; 2A very short and close to wing margin.

The body of this insect has already been described (Carpenter, 1931) and no additional details of structure have been observed since then.

In 1935 one excellent fore wing (3880ab) of this species was found in the upper layer of the limestone. This wing is complete and fully as well preserved as the type. In addition, one very fine specimen (3882) of the hind wing was collected in the upper layer. I have concluded that the latter belongs to *permiana* because it is the proper size and has the required venational characteristics. The strongly arched R + M eliminates it from *Permoscytina*, and its large size shows that it cannot belong to any of the species of *Permopsylla*. On the other hand it is much too small to be the hind wing of *Archescytina muiri* (Till.). *A. permiana* is therefore the only described species to which it can logically belong.

Archescytina muiri (Till.)

Figure 16

Permoscytina muiri Tillyard, 1926, Amer. Journ. Sci., (5) 11: 389.

Permoscytina muiri Carpenter, 1931, Amer. Journ. Sci., (5) 22: 118.

Tegmen: length, 11–12 mm., width, 4 mm.; costal space broad; Rs arising half way between the origin of M and the fork of R1; cell between Cu1a and Cu1b smaller than that of *permiana*. Cu2 terminating at a point nearer to 1A than to Cu1b; 1A smoothly curved at base, not sigmoidal in shape.

Nothing is known of the body structure or of the hind wing. There are no specimens of this species in the 1935 Harvard collection.

I have already given reasons above for transferring this species from *Permoscytina* to *Archescytina*. As Tillyard indicates in his figure of the type, the exact point of fusion of Cu1 with M is not clear, but the joining seems to take place just at the origin of M. The costal margin is shaped as in *permiana*, not arched as figured by Tillyard.

Genus *Permoscytina* Till.

Permoscytina Tillyard, 1926, Amer. Journ. Sci., (5) 11: 387.

Tegmen: slightly convex, very nearly straight, but not concave; Sc close to R1, well developed; R + M straight, not arched towards the anterior margin; Cu apparently free from M at base of wing; free proximal part of Cu1 nearly parallel with R + M, joining M after the latter has separated from R; Cu1 forked distally; two cross-veins, r-m and m-cu, distributed as in *Archescytina*.

Hind wing: very similar to the fore wing, with no obvious differences except that Cu1 is free from M for its entire length. The basal portion of the hind wing is unknown, but 2A is presumably reduced as in the hind wing of the other genera of archescytinids.

Body structure: only the general form of the thorax and abdomen is known. This will be described below.

Permoscytina kansasensis Till.

Figure 17; Plate 1, figure 3.

Permoscytina kansasensis Tillyard, 1926, Amer. Journ. Sci., 11: 388.

Permoscytina kansasensis Carpenter, 1931, Amer. Journ. Sci., 22: 117.

Tegmen: length, 11–12 mm.; width, 3.5 mm. Costal space narrow; pterostigma long and slender; Rs arising at a point much nearer to the pterostigma than to the origin of M; cell between Cu1a and Cu1b about as large as in *A. muiri*; Cu2 probably terminating at a point midway

between Cu1b and 1A. 1A is smoothly curved and both it and 2A are exceedingly strong veins.

One specimen (No. 3881ab) of this species was collected in 1935; it consists of a nearly whole specimen, in dorsal aspect, but unfortunately the head is not preserved. Although the fore wings lie over the hind wings, it is nevertheless possible to distinguish quite easily the veins of each of the wings. Since this is the only specimen of an archescytinid that has been found in which both hind and fore wings are present, it is an exceedingly interesting fossil (Fig. 17). It is this specimen that proves conclusively that Cu is entirely free from M in the hind wing of the archescytinids. Cu1 is easily seen in the fore and hind wings of the right side of the specimen and because of the superimposition of the wings, it can be readily observed that in one wing (fore) Cu1 joins M, whereas in the other wing Cu1 runs directly from the base to the margin. Apparently the other veins are even more alike in the two pairs of wings than is the case in *Archescytina*; at any rate, the veins of both wings seem to coincide throughout, except in the apical region. The posterior and apical margins of the hind wing are not clearly indicated, but presumably the hind wing was somewhat shorter than the fore and more narrowed proximally.

The body of this specimen is not very well preserved for the most part. It is possible to distinguish a broad thorax, 3 mm. long and 4 mm. wide, and a short abdomen, 5 mm. long and 3 mm. wide. The wings were therefore twice as long as the abdomen, and must have extended far beyond the end of the latter when the insect was at rest. Only one segment, the femur, of any of the legs is preserved; the position of this indicates clearly that it is a fore leg. This femur is swollen like that of *A. permiana* (Carpenter, 1931c, fig. 1).

The most striking and extraordinary structure which this fossil shows is a long process, that extends straight back from the end of the abdomen. This is 9 mm. in length and is therefore longer than the thorax and abdomen combined. When I first examined the fossil only a small piece of this structure was visible and I surmised that it was an ovipositor; but after its full length was apparent its nature became more puzzling. It is perfectly obvious that it is not one of a pair of cerci and that it does not consist of the two cerci lying close together, for it is not segmented and has none of the other characteristics of cerci. There are but two interpretations of this structure

that seem at all possible. One is that it is an ovipositor. It is much too long in proportion to the size of the insect, however, to enable us to conceive its use in oviposition. Of course if we assume that it was capable of being arched or coiled, such a function would be more easily imagined; but its appearance is decidedly against that assumption. The fact that it is preserved in a perfectly straight line strongly indicates that it was not flexible, as are the long ovipositors of the parasitic Hymenoptera. Furthermore, if this terminal structure were an ovipositor, it would necessarily represent either the paired first valvulae or paired second valvulae; in which case of course there ought to be some indication of the corresponding pair. Since there is not, we are justified, I think, in concluding that the evidence is decidedly opposed to its being an ovipositor.

The only other interpretation which seems possible is that it is a respiratory tube, similar to that in Recent members of the hemipterous family Nepidae. This view is perfectly consistent with the straight and rigid appearance of the terminal process in the fossil, and especially with its median longitudinal division, for of course the respiratory tube of the Nepidae is formed by the application of a pair of grooved processes. A comparison of the respiratory tube of the nepids and the terminal process of the fossil reveals such striking similarities of formation, that I believe we are justified in attributing a similar function to the structure in the fossil.^{16a}

This conclusion, of course, presupposes that the insect was aquatic. So far as known at present, there is no indication of modification of the rest of the body for an aquatic environment. Both pairs of wings are broad and their nature is hardly consistent with what we should expect in an aquatic species. It seems likely, therefore, that these insects were aquatic in their nymphal stages, before the wings were fully developed; and that the adults, although retaining the respiratory tube, were terrestrial and capable of active flight. In this connection it should be noted that, apart from the modification of the respiratory system, the nepids are not adapted to an aquatic existence, their fore legs being rpto-

^{16a} It should perhaps be pointed out that this process can not be part of the beak because the latter is known to be much too short in the Archescytinidae to extend even to the tip of the abdomen; and because the origin of the process from the abdomen is very clear in the fossil.

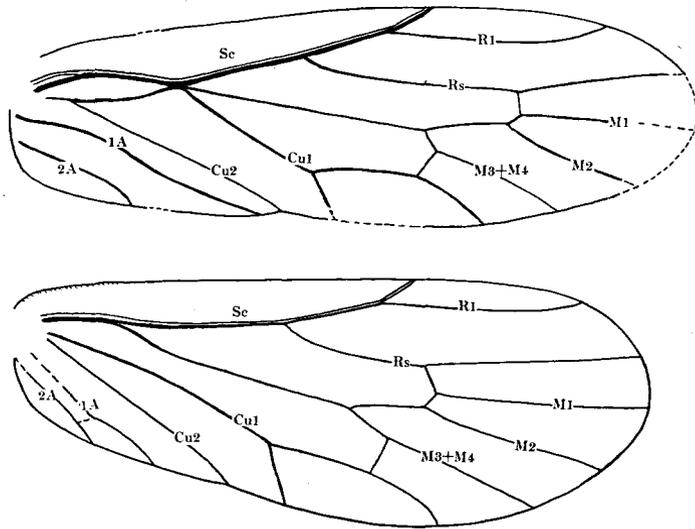


FIGURE 15. *Archescytina permiana* Till.; fore wing drawn from holotype, No. 5111, Peabody Museum, Yale University; hind wing drawn from specimen No. 3882, Museum of Comparative Zoölogy.

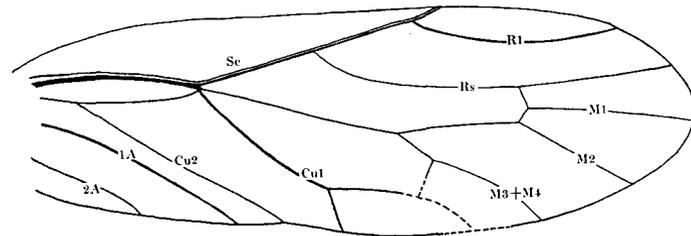


FIGURE 16. *Archescytina muiri* (Till.), fore wing, drawn from holotype, No. 5113, Peabody Museum, Yale University.

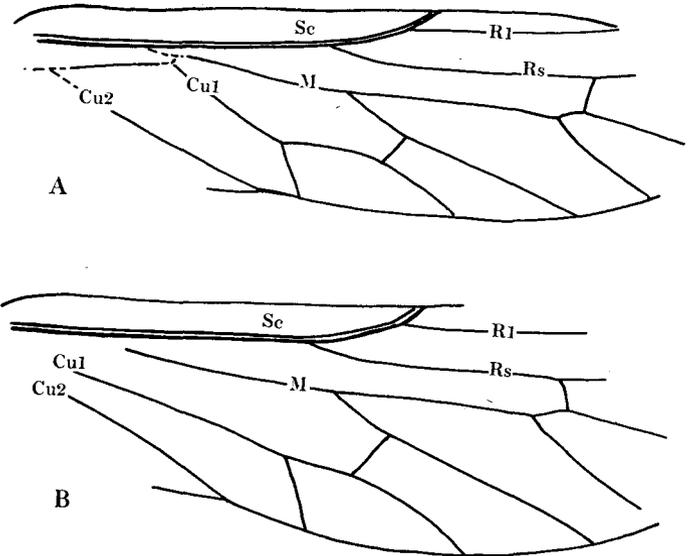


FIGURE 17. *Permoscytina kansasensis* Till., drawing of fore and hind wing; specimen No. 3881ab, Museum of Comparative Zoölogy.

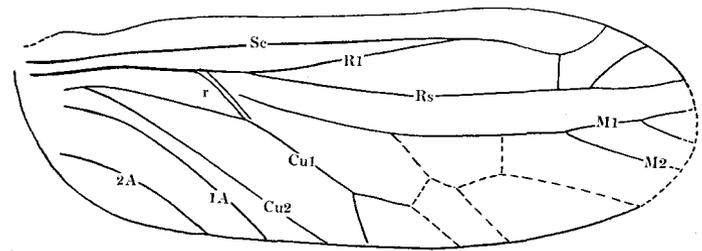


FIGURE 18. *Lithopsocidium permianum* Carp., drawing of venation, specimen No. 4322ab, Museum of Comparative Zoölogy.

rial and the others cursorial. We know nothing, unfortunately of the meso- and metathoracic legs of *Permoscytina kansascensis*, but in the very closely related *Archescytina permiana*, the middle and hind legs were fitted for walking, and the fore legs were raptorial. The latter assertion is based upon the fact that the fore tarsi terminated in a single stout claw (Carpenter, 1931c, fig. 1), and the femur was much swollen, and possessed a row of stout spines along the outer margin. All we know of the fore leg of *Permoscytina kansascensis* is the femur which is preserved in the specimen under discussion (3881); but, as previously mentioned, that is swollen as it is in *A. permiana*. I believe therefore the available evidence indicates that *Permoscytina* was an aquatic insect at least in the nymphal stages, breathing by means of a respiratory tube like that of the Nepidae, and feeding on prey which it captured by means of the raptorial fore legs. Also, although we have not yet found any specimens of *Archescytina* which show a respiratory tube, I believe that the members of this genus were likewise aquatic, since the two genera were obviously very closely related, and *A. permiana* also had raptorial fore legs.

The foregoing discussion does not intend to imply a close phylogenetical relationship between the hemipterous (heteropterous) family Nepidae and the homopterous genus *Permoscytina*. That such a relationship has not existed is perfectly obvious. The significant fact (assuming the above interpretation is correct) is that in the Lower Permian an abdominal respiratory tube was developed in the Homoptera which apparently served the same purpose as that which now occurs in the Nepidae. The presence of this structure is another instance of the parallel evolution which has taken place so frequently in unrelated families of insects.

Genus *Permoscytina* Till.

Permoscytina Tillyard, 1926, Amer. Journ. Sci., (5) 11: 390.

Permoscytina Carpenter, 1931, Amer. Journ. Sci., (5) 22: 119.

Tegmen: anterior margin slightly concave opposite origin of M, sometimes almost straight, but never convex; Sc close to R + M and R1, weakly formed; R + M arched towards anterior margin; free proximal piece of Cu1 straight, directed anteriorly, fusing with M close to its origin. Cu2 forked; 1A nearly straight; 2A generally curved sigmoidally.

The hind wing of this genus is apparently like that of *Archescytina*. One of the 1935 specimens of *Permoscytina minuta* Carp. (No. 3878ab) has a part of the hind wing preserved, and shows that Cu1 is entirely independent of M. The species which I previously described (1931) as *Lithoscytina cubitalis* is obviously a hind wing of some species of *Permoscytina*, presumably *P. grandis* Carp. This specimen shows the characteristic cubitus of the hind wing. It also shows a relatively straight R (or R + M), and this same peculiarity is even more clearly indicated in the specimen of *minuta* mentioned above.¹⁷ 2A is very close to the hind margin, as in the hind wings of the other genera of Archescytinidae.

Almost nothing is known of the body structure of these insects, their small size greatly reducing the chances of good preservation. The new specimen of *P. minuta* mentioned above (No. 3878) is the only one so far found which shows any of the body and no details are discernible. The entire body is only 2 mm. long, with a maximum width of .8 mm. Since the wings are about 2.5 mm. long they obviously extended beyond the end of the abdomen in the position of rest. There appears to be a terminal process extending from the abdomen, but its form is very obscure.

Twenty-three specimens belonging to this genus were secured in 1935; all but three of these were found in the upper layer of the limestone, confirming my earlier statement that the order Homoptera is probably more abundantly represented in the upper layer than the lower. *P. americana* Till. is represented by seven good fore wings, two being from the lower layer. Two of the wings are especially well preserved (No. 3860ab, 3861ab). Eight specimens, all from the upper layer belong to *P. permiana* Carp., two of the lot (No. 3878ab, 3875ab) being excellently preserved. The largest species of the genus, *grandis*, is represented by four fossils consisting of fore wings, all from the upper layer; three of these (Nos. 3867ab, 3869ab, and 3770ab) are splendidly preserved. The smallest species, *minuta*, includes two fine specimens; one (No. 3877ab) is a fore wing from the upper layer, and the other (No. 3878ab, lower layer) is the more

¹⁷ The proximal portion of R is probably even more nearly straight in the hind wing described as *Lithoscytina* than it is represented in my figure (1931c, fig. 9). That part of the wing was not very clearly preserved, and since the new specimen of *minuta* has the proximal part of R almost exactly straight, the same was probably true of the former hind wing.

nearly complete specimen already mentioned, showing a fore wing, part of a hind wing, and the body.

THE AFFINITIES OF THE ARCHESCYTINIDAE

In addition to the foregoing Lower Permian species, the family Archescytinidae also includes several described by Martynov (1933) from the upper Permian of Russia. Certain changes must now be made in the generic disposition of Martynov's species, however, to conform with the corrections noted above in the genotypes of *Archescytina* and *Permoscytina*. *Permoscytina sojanensis* Martynov and *P. tetracлада* Martynov obviously do not belong to *Permoscytina*, since the stem R + M is strongly arched. As Martynov mentioned, both of these species were very close to *muiri* Till., rather than to the genotype of *Permoscytina*, i. e., *kansasensis*. The removal of *muiri* to *Archescytina* must therefore be followed by the transfer of both *sojanensis* and *tetracлада* to *Archescytina*. The genus *Sojanoscytina* Martynov is clearly close to *Archescytina*, rather than to *Permoscytina*, but remains a distinct genus on the basis of the structure of the anal veins as well as the media. However, the hind wing which Martynov describes as *Sojanoscytina* (?) *latipennis* can hardly belong to any member of the family Archescytinidae, since it has Cu1 joined to M as in the fore wings. If it should turn out that the species of *Sojanoscytina* actually did possess such a hind wing as he describes as *latipennis*, then the genus will require a new family for its reception. The free Cu1 now known to have existed in *Archescytina*, *Permoscytina*, and *Permopsylla*, indicates a very different line of evolution from that depicted by the fused Cu1 in *S.* (?) *latipennis*.

In 1931 I pointed out that the Archescytinidae appeared to possess certain characteristics which eliminated them from both the existing divisions (Sternorrhyncha and Auchenorrhyncha) of the Homoptera and I therefore established for them the division Paleorrhyncha. Martynov, however, believes (1933) that the archescytinids are nevertheless closer to the Sternorrhyncha than to the Auchenorrhyncha. He concedes that the 3-segmented tarsi of the Archescytinidae excludes them from the Sternorrhyncha, but expands the definition of the Sternorrhyncha to include Homoptera with 3-segmented tarsi in order to embrace the Archescytinidae. It is of course purely an arbitrary matter in these cases whether one prefers to modify the conception of

an existing category to include such extinct groups or to establish a parallel category especially for them. The choice in the matter presumably depends upon the amount of modification that may be necessary, and there can be no hard and fast lines drawn between the two procedures. In the case of the Archescytinidae I personally prefer to regard them as members of a distinct division, rather than to modify our conception of the Sternorrhyncha in order to include them there.

Martynov's conclusion that the archescytinids stand very close to the true Sternorrhyncha (especially the Aphidoidea) now appears hardly justifiable. His assumption that the isolated hind wing described as *Sojanoscytina* (?) *latipennis* belonged to the Archescytinidae seems to be quite incorrect, in view of the nature of the hind wings found attached to the new specimens described above from the Elmo limestone. The discovery that *Permoscytina* (and presumably all the Archescytinidae) were aquatic at least as nymphs, possessing an abdominal respiratory tube, shows also that this particular family was not ancestral to either of the existing divisions of the Homoptera. However, it is obvious that this modification was only an adaptation to an aquatic existence, and that their fundamental characteristics (such as the 3-segmented tarsi, the complete clavus, and the multisegmented antennae) were not concerned with their aquatic specializations. An homopteron possessing such fundamental features, but not specialized for an aquatic life, would be a more typical member of the division Paleorrhyncha and might conceivably be in the common ancestral line of both existing divisions.

After the manuscript of the present paper had been completed, I received a recent publication by G. Zalesky (1937), in which the author establishes the Order Hemipsocoptera for a new fossil, *Maueria sylvoensis* Zal., from the Permian of Russia. This specimen, although not very well preserved, consists of a nearly complete insect, the wings being outstretched and the body faintly indicated. As is apparent from the name of the new order, Zalesky considers the fossil to represent an order intermediate between the Psocoptera and the Hemiptera. It is at once obvious, however, even from an examination of Zalesky's diagrammatic figures of the wings, that the fossil is a typical archescytinid, undoubtedly belonging to *Archescytina* itself or one of the other genera of the family which have already been found in the

Russian Permian! Zalessky was led to attribute psocopterous affinities to this fossil because of the hind wing, which has *Cu*₁ free, as it is now known to be in the archescytinids. The family Maueriidae is obviously a synonym of Archescytinidae and the genus *Maueria* is here placed as a synonym of *Archescytina*. The incomplete preservation of the wings of the fossil makes the exact course of the veins obscure, so that the specific characteristics are necessarily uncertain. It is very unfortunate that Zalessky should have erected a new order for a unique and poorly preserved specimen, especially since he had previously established another invalid order (Permodonata) on equally insufficient material. A new order of fossil insects, as Tillyard has pointed out (1931, p. 232), should be avoided as far as possible, and not be made as soon as the slightest pretext is offered. The body structure of the Archescytinidae (Maueriidae) shows beyond question that they were true Hemiptera, even though the hind wings contained some suggestions of the Psocoptera.

Order PSOCOPTERA

194 specimens of Psocoptera were collected in 1935, bringing the total number of these insects in the Museum of Comparative Zoölogy to 487. Only seventy of the new fossils were found in the lower layer. In addition to the species discussed more fully below, *Dichentomum latum* Carp., *D. grande* Carp., and *Progonopsocus permianus* Till. are represented in the new material, the first by six specimens (five upper, one lower layer); the second by five (three upper, two lower layer); and the third by four (two upper, two lower layer).

Family DICHENTOMIDAE

In a very recent paper (1937) Zalessky discusses in some detail the classification of the Psocoptera of the Elmo limestone and takes issue with me on the synonymy and classification of certain species. In the first place he believes that the family name Psocidiidae should be employed instead of Dichentomidae. The family Psocidiidae was established by Tillyard in 1926 for six genera in the Elmo limestone, which he described in the following order: *Dichentomum* (p. 320), *Psocidium* (p. 321), *Chaetopsocidium*, *Metapsocidium*, *Pentapsocidium* and *Permentomum*. A study of Tillyard's types of the species belonging to these genera, as well as a great many more specimens, led me to conclude (1932, pp. 3-6)

that the five latter genera (*Psocidium*, *Chaetopsocidium*, *Metapsocidium*, *Pentapsocidium*, *Permentomum*) were synonyms of *Dichentomum*. The family name was of course changed to Dichentomidae, since *Psocidium* was a synonym of *Dichentomum*. Now Zalessky, although admitting that the foregoing genera are synonymous, makes the extraordinary statement (p. 70) that in uniting these genera the generic name *Psocidium* should be used, thus retaining the family name Psocidiidae. Such a procedure would of course be contrary to the rules of priority of names,¹⁸ and I am utterly unable to understand how Zalessky could make such a proposition unless he is totally unaware of the existence of such rules. Tillyard himself in a later paper (1935, p. 267) accepts the synonymy of *Psocidium* with *Dichentomum* and of course states that the family name should be Dichentomidae.

Although Zalessky agrees with my synonymy of Tillyard's genera of the Elmo Psocoptera, he rejects my synonymy of the species. Unfortunately, he has completely failed to note that many of the species concerned (*Chaetopsocidium sellardsi*, *Metapsocidium loxonerum*, etc.) were incorrectly described or figured by Tillyard, as I pointed out in detail (1932, pp. 4-6). He has obviously not taken into account my correction of the descriptions of these species in his attempt to classify the Elmo Psocoptera; this is well shown by the fact that he illustrates his paper with copies of two of Tillyard's figures (*Psocidium permianum* and *P. kansasense*) without mentioning my corrections of them (1932, pp. 8-9). It is this same oversight on Zalessky's part which leads him to ask why *D. latum* Carp. is not a synonym of *D. tinctum*, inasmuch as the various species which Tillyard described and which I regarded synonyms of *tinctum* show so much diversity of venation. The simple fact, of course, is that Tillyard's species do not have the diversity that was attributed to them, but show differences which are trivial and occur in the right and left wings of the same individual! But in the course of my examination of more than four hundred specimens of *Dichentomum* I have found none intermediate in structure between *tinctum* and *latum*. It is unfortunate that Zalessky undertook to revise the synonymy of the Psocoptera in the Elmo limestone, especially since he has never seen a single specimen from the formation.

¹⁸ International rules of Zoological Nomenclature, articles 25 and 28.

Dichentomum tinctum Till.

Plate 2, figure 6

Dichentomum tinctum Tillyard, 1926, Amer. Jour. Sci., (5) 11: 320.

Dichentomum tinctum Carpenter, 1932, *ibid.*, 27: 70 (complete synonymy given here).

Dichentomum tinctum Carpenter, 1933, Proc. Amer. Acad. Arts Sciences, 68: 443.

164 specimens of this insect were collected in 1935, more than on any previous trip. The total number of specimens of this species now contained in the Museum of Comparative Zoölogy is about 390. Most of the new fossils are of course isolated fore or hind wings and need no further comment; but a few are especially interesting because of the body structures preserved. Five of the specimens (4328ab, 4329ab, 4330ab, 4331ab, 4334ab) show clearly the rostrum, which I have previously described in this species. One specimen (No. 4332ab), preserved in lateral view with one of the wings outstretched, is of even greater interest because genital structures are distinctly visible. These appendages, which are .6 mm. long apparently consist of a pair of curved hooks (Plate 2, figure 6), and are presumably homologous with the copulatory hooks occurring in the males of some Recent psocids (cf. Plate I, figs. 5, 6 of Enderlein's "Copeognatha" of Collections Selys, Fasc. III (2), 1919). The apparent absence of the hooks in the specimens of *D. tinctum* previously studied is undoubtedly the result of their failure to be preserved. Because of the small size of these insects optimum preservation is necessary to show such details.

Lithopsocidium permianum Carp.

Figure 18

Lithopsocidium permianum Carp., 1932, Amer. Journ. Sci., 24: 14; fig. 7. 1933, Proc. Amer. Acad. Arts Sci., 68: 449, fig. 15.

A third specimen (No. 4322ab) of this rare insect was collected in the upper layer of the limestone in 1935. Like the others, this one consists of a single wing, and is not very well preserved; but it is of much interest because the area around the origin of M is much clearer than in the other two specimens, and shows distinctly a certain peculiarity not previously described. The stem of R in all three fossils is strongly convex, and in the new specimen there is a similar strongly convex ridge leading from R, at a point slightly proximal of the origin of Rs, to Cu1 (figure 18).

An examination of the other two specimens of *L. permianum*, including the type, shows that a similar oblique ridge is likewise present in them, but presumably because of the poor preservation of that area of the wings, they were not considered as part of the wing when I described them. The new fossil clearly demonstrates that the ridge is a definite structure in the wing. I am at a loss to explain its nature. In none of the specimens is this ridge preserved as a dark line as are the veins in the wing; it is the same color as the membrane. Also there is no vein in the wings of the other Psocoptera with which it might be considered homologous. The relationship between the ridge and the base of the media is obscure. In none of the specimens of *permianum* is the origin of the media clear, but this is likewise true of the other Permian Psocoptera, even *Dichentomum tinctum*, of which a great many specimens have been collected. Whatever the nature of this ridge may be, it is undoubtedly a constant feature of the wing and should be added to the generic characteristics.

The new specimen of *permianum* substantiates the conclusion that the costal margin is curiously curved and unlike that of the other Permian Psocoptera. The costal area of the new fossil is not well preserved and the several cross-veins, previously noted in another specimen, are not visible. In my previous discussions of *Lithopsocidium*, I have assumed from the shape of the wing that the specimens were hind wings; this also applies to the new specimen, but the differences in the fore and hind wings of the other Permian Psocoptera are so slight that this is hardly more than an assumption.

Family PERMOPSOCIDAE

Permopsocus latipennis Tillyard

Plate 2, figure 5

Permopsocus latipennis Tillyard, 1926, Amer. Journ. Sci., (5) 11: 340. Carpenter, 1932, *ibid.*, 24: 13 (complete synonymy given here).

Five specimens of this species were collected in 1935, all except one in the upper layer of the limestone. Only one of these deserves comment (No. 3992ab). This consists of a more or less complete specimen preserved in lateral aspect with two wings outstretched. The interesting feature of this fossil is the presence of a conspicuous process at the end of the abdomen (plate 2, fig. 5). This apparently arises from the region of the ninth sternite and is 1 mm. long. Although

in its general appearance it resembles an ovipositor, I believe that it represents one of a pair of male copulatory appendages, homologous with the hooks just described in *D. tinctum*. This conclusion has been reached because not only is the process bluntly rounded distally, but it has the false joint near its middle characteristic of the male copulatory structures (e.g., styli of male Plectoptera), and apparently also has the false terminal segments. The presence of such copulatory processes in *Permopsocus* would not be unexpected in view of their existence in *Dichenotomum*.

***Permopsocus ovatus*, new species**

Figure 19

Fore wing: proportionally broader than in *P. latipennis*; length, 4.5 mm.; width, 1.8 mm. Sc with only slight bend at the base, as in *P. latipennis*; costal space broad, much more so than in *P. latipennis* and closer to R1 than in the latter; ir1 strongly oblique, ir2 slightly inclined; two cross-veins are present (in the type specimen) between Rs and M, but as in the case of *P. latipennis*, their presence is probably an individual characteristic only; areola postica very large, wider than high; 2A apparently longer than in *P. latipennis*.

Holotype: No. 4336ab, Museum of Comparative Zoölogy; collected by the writer in the upper layer of the Elmo limestone, 1935.

This species, although close to *latipennis*, differs chiefly in the much larger and wider areola postica and in the proportionally broader, sub-oval wing. The shape of the wing might, by itself, be regarded as an individual characteristic, but the large areola postica cannot be so considered, especially since specimens of *latipennis* present very little variation in the shape of this cell. The presence of the chitinous lobe at the base of the posterior margin shows that the type of *ovatus* is a fore wing.

Family CYPHONEURIDAE

In 1932 I described two very small and remarkable wings from the Elmo locality as *Cyphoneura permiana* and *C. reducta*, placing the genus close to *Lophioneura* Till. from the Upper Permian of Australia. The latter genus had been assigned to the Homoptera by Tillyard, who believed that the family it represented (Lophioneuridae) was directly ancestral to the Chermidae (Psyllidae). I accordingly assigned the family Cyphoneuridae to the Homoptera, although I noted that the

venation of these wings contained many suggestions of that of the Psocoptera.

More recently (1935) Tillyard has studied and described a number of other specimens from the Australian Permian related to *Lophioneura* and *Cyphoneura*, and concludes from the body structure preserved with the additional wings that the insects were Psocoptera, not Homoptera. If Tillyard's figures correctly depict the head structure of these insects, there can be no doubt of the psocopterous affinities of the fossils, and I accept Tillyard's conclusion with that assumption. I do not, however, agree with Tillyard on the classification of these peculiar insects. He maintains that all of the Psocoptera possessing "a sigmoid Cu1 and abnormal origins of Rs, M and Cu2" should be placed together in the family Lophioneuridae, thus eliminating the family Cyphoneuridae. On this basis, however, one of the Kansas species, *C. reducta*, which possesses a perfectly straight Cu1, is eliminated from the Lophioneuridae, although Tillyard placed it there. Furthermore, the expression, "abnormal origins of Rs, M and Cu1," is too vaguely inclusive to be of any aid in classifying these insects. Much more significant, in my opinion, is the fact that the species of *Lophioneura* (*ustulata* and *angusta*) differ strikingly from those of all other genera of Psocoptera by the complete absence of Cu2 as an independent vein. Such a marked difference certainly seems to require family distinction, the Cyphoneuridae including those species with Cu2 present as a free vein, and the Lophoneuridae, those species lacking Cu2. On this basis *Cyphoneura*, *Astrocypha*, and *Lophocypha* are here placed in the family Cyphoneuridae; and *Lophioneura* in the family Lophoneuridae.

Family DELOPTERIDAE

Only fourteen species of this family were collected in 1935. This small number of specimens is undoubtedly due to the fact that most of the collecting was done in the upper layer of limestone, in which the Delopteridae are much less common than they are in the lower layer. Of this series of specimens only one (*Delopterum latum* Till. No. 3989) was found in the lower layer.

Delopterum minutum Till. is represented by two specimens.^{18a} No. 3978 is a complete and well

^{18a} Since *Pseudomantis* Martynov is a synonym of *Delopterum* (Carpenter, 1933, p. 452), it is necessary to designate a new name for *Ps. minuta* Mart. (Permian of

preserved fore wing; No. 3979 is a complete specimen, in dorsal view, showing the wings outspread and the body very well, although no legs are visible. This fossil has the abdomen better preserved than any other specimen that has been collected, and it is especially interesting because it shows a pair of small but distinct cerci (Plate 2, fig. 3).

In neither of the new specimens am I able to make out the oblique vein between R1 and R2 + 3, which is present in at least some specimens previously collected and studied. The presence or absence of this vein may be a matter of individual variation rather than of specific nature, unless of course very fine preservation is needed to show it.

Delopterus elongatum Sell. is represented in the new material by 11 specimens (No. 3979-3988), which is about twice as many individuals as have previously been known. Nearly all of these are isolated fore wings and deserve no further comment. It should be noted that some of these wings are only a little over 5 mm. long, which is very near to the maximum size of *minutum*. The length of the subcosta seems to be variable, though it is usually longer in *elongatum* than it is in *minutum*. The occurrence of so many specimens of *elongatum* substantiates the tentative conclusion based on the 1932 material, that this species is much commoner in the upper layer than in the lower layer of the limestone.

Delopterus latum Sell. (figure 20) is represented by a single, well preserved wing from the lower layer (No. 3889). In all probability this species does not occur in the upper layer; at any rate no specimens of it have been found there so far. While there is a possibility that *minutum* and *elongatum* are synonyms, *latum* is very readily distinguished by the sigmoidal form of 2A and its branch leading to the hind margin.¹⁹ In this species also the forking of M takes place much

nearer its origin than it does in the other species, and as a consequence the anterior branch, M1 + M2, is very close to Rs proximally. As a matter of fact the actual basal connection of M1 + M2 is not discernible in any of the specimens which have been collected and it may be that this part of the vein has been atrophied or arises from Rs.

Delopterus kansanum, new species

Figure 21

Fore wing: length 6 mm.; width, 1.8 mm. Costal margin distinctly convex, with a slight concavity near the base of the wing; Sc remote from anterior margin and long, extending far beyond the middle of the wing and nearly to the end of R1; M arising from Cu1 a little proximad of the origin of Rs; M dividing close to its origin as in *latum*, but with M1 + M2 remote from Rs; areola postica lanceolate, Cu1 forking dichotomously; 2A sigmoidally curved, as in *latum*, but longer.

Holotype: No 3990ab, Museum of Comparative Zoölogy; collected by the writer in the upper layer of the Elmo limestone (1935). The type specimen consists of a complete and very well preserved fore wing.

This species is close to *latum*, but differs primarily by the longer Sc, the much broader costal area, the remoteness of M1 + 2 from Rs, the lanceolate areola postica and the longer 2A. It may be that some of these characteristics, such as the form of the areola postica, will turn out to be individual ones; but others, such as the length of Sc and the width of the costal area, can hardly belong in this category.

The affinities of the family Delopteridae are still uncertain. In my previous paper I reviewed the evidence bearing on this subject, and have shown that it indicates a close relationship with the Psocoptera, as originally concluded by Tilliard. Unfortunately, we have very little knowledge of the head structure, aside from the fact that a rostrum, like that of the Dichentomidae, was not present.

Order PROTELYTROPTERA

Thirty-three specimens of Protelytroptera were found in 1935, making a total of eighty-nine in the Museum of Comparative Zoölogy. The new fossils contribute materially to our knowledge of the structure of the elytra, especially in the obscure family Blattelytridae.

Tikhie Gory, Russia) that specific name having been used for the genotype of *Delopterus*. I brought this to Dr. Martynov's attention in 1937 and he wrote in November of that year that he would propose the name *kamense*. Since he died a few weeks later without being able to prepare a note for publication, I take this opportunity to make that designation: *Delopterus kamense*, n. n., for *Delopterus (Pseudomantis) minutum* Martynov (1928), nec *D. minutum* Sellards (1909).

¹⁹ Martynov has placed *latum* in a separate genus, *Pseudodelopterus* (1928, p. 66, foot-note), but I do not believe there are enough differences between this species and the foregoing to justify generic separation.

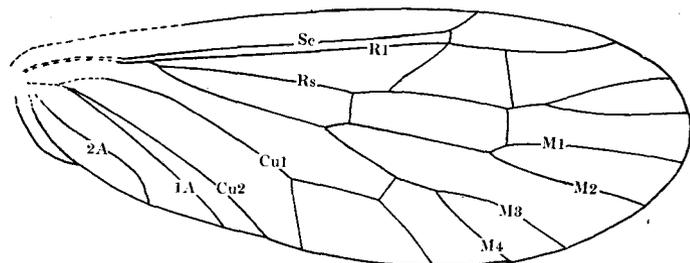


FIGURE 19. *Permpsocus ovatus* n. sp., drawing of fore wing; holotype, No. 4336ab, Museum of Comparative Zoölogy.

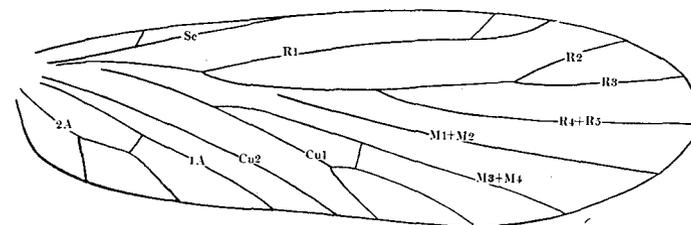


FIGURE 20. *Delopterus latum* Sell., drawing of fore wing; specimen No. 3889, Museum of Comparative Zoölogy.

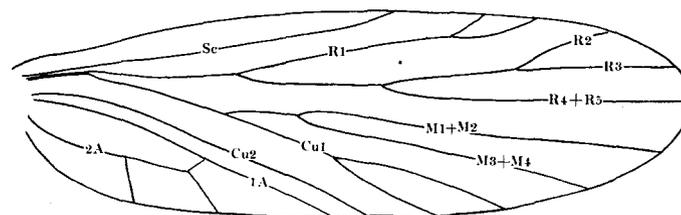


FIGURE 21. *Delopterus kansanum*, n. sp., drawing of fore wing; holotype, No. 3990, Museum of Comparative Zoölogy.

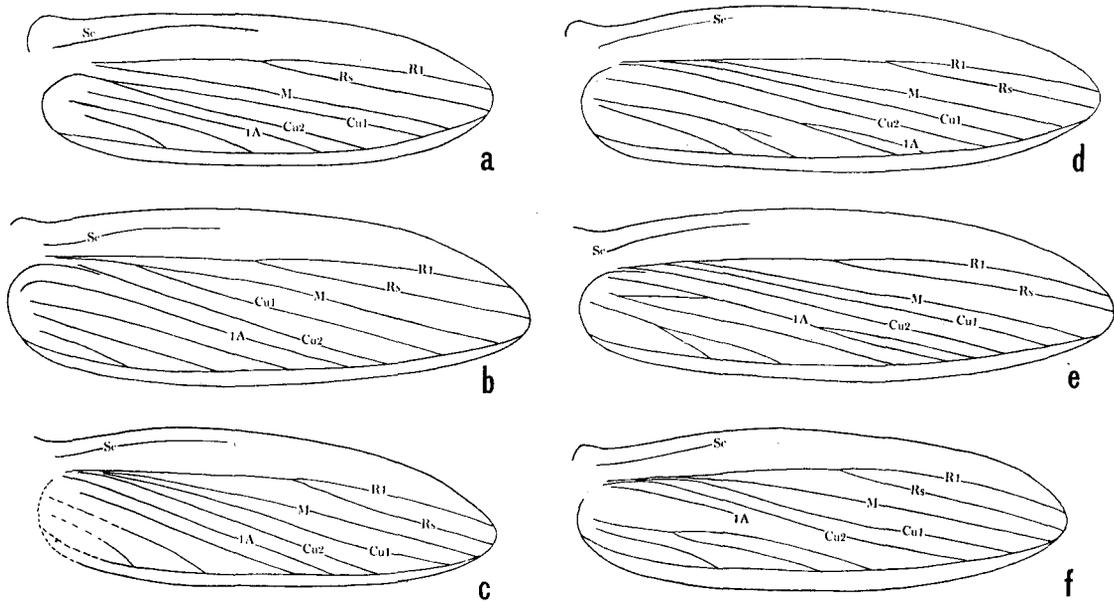


FIGURE 22. *Protelytron permianus* Till., venation of elytra; a, specimen No. 3266; b, No. 3889; c, No. 3893; d, No. 3884; e, No. 3883; f, No. 3892.

Family PROTELYTRIDAE

Genus *Protelytron* Till.

Protelytron Tillyard, 1931, Amer. Journ. Sci., (5) 21: 239.

Protelytron Carpenter, 1933, Proc. Amer. Acad. Arts Sci., 68: 465.

Protelytron permianum Till.

Figure 22

Protelytron permianum Tillyard, 1931, Amer. Journ. Sci., (5) 21: 240; figs. 1-3, 14, 15.

Protelytron permianum Carpenter, 1933, Proc. Amer. Acad. Arts Sci., 68: 467; figs. 17, 18.

Protelytron tillyardi Carpenter, 1933, Proc. Amer. Acad. Arts Sci., 68: 473, fig. 19.

In the new material there are ten specimens belonging to this species, five of which have a venation in the elytra which is typical of the species (Carpenter, 1933, fig. 17): Nos. 3886, 3887, 3888, 3890, 3891 (all from the upper layer except the last). The venation of the other five specimens, however, is not like that which has previously been recognized in *permianum*, the differences being mainly in the branches of M and Cu. In the typical elytra of *permianum* (figure 22a) M is free from R for its entire length, arising near the base of the elytron; similarly, Cu arises independently, and gives rise to Cu1 and Cu2 at the very base of the elytron. Cu2 coincides or

very nearly coincides with the *vena dividens*, which is clearly indicated proximally. In the first of the atypical elytra mentioned (figure 22b, No. 3889, lower layer) the venation differs from the foregoing in that Cu1 is coalesced with the proximal part of M, so that M appears to be deeply forked. In the second elytron (figure 22c, No. 3893, upper layer), R, M and Cu are all coalesced proximally, and all arise independently from this common stem. In the third elytron (figure 22d, No. 3884, upper layer), Cu1 is coalesced with M as in b above, but M is also fused proximally with R. In the fourth elytron (figure 22e, No. 3883, upper layer), the structure is exactly as in d, except that Cu2 is slightly coalesced with the stem of R also. In the fifth elytron (figure 22f, No. 3892, upper layer), Cu1 is free from M, but M is coalesced with R.

It is apparent from our examination of these elytra that the structure of R, M, Cu1 and Cu2 is subject to much individual variation, comparable to a certain extent to the variation which occurs in the family Lemmatophoridae (Order Protoperlaria). There seems to be no justification for regarding these differences as of a specific nature, because they show so many intermediate conditions. If our study of the venation of these elytra is extended to include other species and genera, it also becomes apparent that the evolution within the family Protelytridae has largely

been concerned with changes in the proximal structure of R, M, and Cu. The starting point of this evolution seems to be represented by the typical venation of *permianum*. From this point there seem to have been two lines of evolution. One of these, represented in *permianum*, is exemplified by the tendency for M and Cu to coalesce with R. The other line, represented in *Protelytron furcatum* n. sp. (figure 23a) is in the direction of the coalescence of Cu1 and Cu2 for a considerable distance from the base of the elytron. This line reaches its extreme development in *Permelytroptis*, in which Cu1 and Cu2 have entirely coalesced (Carpenter, 1933, fig. 21).

To return to the elytra of *permianum* shown in figure 22, it should be noted that there is considerable variation in the structure of the anal veins. A fourth anal vein is present in some of the elytra, but this is often very feebly developed. There is also a tendency for the anal veins to be forked, as in d and e, figure 22. These forkings seem to occur in a haphazard manner, indicating that they are mere individual fluctuations. The condition of the anal veins in the specimen shown in figure 22f is decidedly different from that of any of the other elytra which I have seen; but it should be noted that the structure of 1A in this fossil is strongly suggestive of abnormal conditions. Since similar variations (exclusive of the last) are to be found in the elytra of *permianum* which are otherwise typical of the species, I am led to conclude that we have here but another instance of the unusual amount of individual variability of the Permian insects to which I have previously referred.

These new specimens of *permianum* indicate that there is also considerable variation in the shape of the elytron and the width of the sutural margin. I am therefore of the opinion that *P. tillyardi* Carp., which was based on an unusually broad elytron with a very wide sutural margin, is also a specimen of *permianum*. *P. angustum* Carp. is almost certainly a distinct species; its sutural margin is so exceedingly narrow and the elytron as a whole so long that it seems beyond the limits of variation of *permianum*.

Protelytron furcatum, new species

Figure 23A

Elytron: length 6-7 mm.; width 2 mm. Costal margin convex, apex rounded; Rs arising slightly beyond the middle of the wing; base of M either coalesced with R or independent; Cu free from M,

dividing with Cu1 and Cu2 almost at the middle of the wing; 4 anals present (in types); sutural margin of moderate width.

Holotype: No. 3885ab, Museum of Comparative Zoölogy; collected by F. M. Carpenter in the upper layer of the limestone. This specimen consists of a splendidly preserved elytron.

Paratype: No. 4366ab, Museum of Comparative Zoölogy; collected by F. M. Carpenter in the lower layer of the limestone. This is a single elytron, not so well preserved as the holotype.

These two elytra undoubtedly represent a species distinct from *permianum*, characterized by the late separation of Cu1 and Cu2. None of the numerous specimens of *Protelytron* which I have seen have showed a structure of the cubitus intermediate between that in *furcatum* and *permianum*.

Family BLATTELYTRIDAE

This family is represented in the new material by twenty-three specimens, most of which are especially well preserved. A study of these elytra shows that a modification of our present conception of this family is needed. The chief and almost the only characteristic which has distinguished the family Blattelytridae from the Protelytridae is the obsolescent nature of the main veins in the distal part of the elytra. The excellently preserved new specimens of Blattelytridae now show that in some species at least the venation was better developed than has previously been supposed. In *Permelytron* and *Acosmelytron subincisum*, for example, the veins extend almost as far distad as they do in *Protelytron*. The difference between the venation of these two families lies in the fact that even in the best preserved of the Blattelytridae the veins of the *entire* elytron are very weakly developed. Since drawings of the venation cannot depict this quality of the venation, they are very deceptive, indicating a closer resemblance between the elytra of the two families than actually exists. Apart from the obsolescent nature of the blattelytrid venation, the family is also distinguished by the total absence of Rs.

The new specimens of Blattelytridae also indicate that some changes are required in our conception of the genera of the family. In 1933 I placed here four genera: *Blattelytron*, *Permelytron*, *Acosmelytron*, and *Parablattelytron*. The first of these genera was based upon so small a fragment that in all probability additional specimens of this species will not be recognizable as such. All

the remaining genera are represented in the new material, and the excellent specimens included show that the elytra of all genera had a better developed venation than we have assumed was present. It also becomes apparent that *Parablattelytron* Till. can no longer be regarded as distinct from *Acosmelytron*.

Permelytron schucherti Till.

Figure 23B

Permelytron schucherti Tillyard, 1931, Amer. Journ. Sci., (5) 21: 247; fig. 6.

A very well preserved elytron (No. 4344) of this specimen was found by the writer. This is much better preserved than the type, which has thus far been the sole representative of this species, and enables us to define the species more satisfactorily. The elytron is 8 mm. long and 2.5 mm. wide, which is exactly the same size as the type. I have already pointed out (1933, p. 463) that the sutural margin of the type was formed as in other members of this family, not narrow distally as described by Tillyard. The costal expansion is well developed and the elytron is shaped as in the other Blattelytridae. Sc is long, as in *Acosmelytron*, and R is strongly formed, though there is no Rs present; M is weakly developed; the branches of Cu are coalesced almost as far as the middle of the wing; they terminate far distad of their origin; only the first anal vein is apparent and that is very poorly developed. The sutural margin is narrow.

Genus *Parablattelytron* Till.

Parablattelytron Tillyard, 1931, Amer. Journ. Sci., (5) 21: 251.

Parablattelytron Carpenter, 1933, Proc. Amer. Acad. Arts Sci., 68: 482.

Acosmelytron Tillyard, 1931, Amer. Journ. Sci., (5) 21: 253.

Acosmelytron Carpenter, 1933, Proc. Amer. Acad. Arts Sci., 68: 480.

The two genera, *Parablattelytron* and *Acosmelytron*, were originally separated by Tillyard into different families. In 1937 I placed them both in the single family Blattelytridae, and I now think it necessary to synonymize these two genera. The difference which Tillyard considered to be of family significance, and which I regarded as of generic rank, does not exist. This supposed distinction was that in *Acosmelytron* Cu1 was present and Cu2 was absent; whereas in *Parablattelytron* Cu1 was absent and Cu2 was present.

The determination of these veins was made on the basis that Cu1 was convex and Cu2 concave. It now becomes apparent that only the *vena dividens*, or at the most Cu2, is present in either of these genera, the slightly convex ridge which we had interpreted as Cu1 being the result of the breaking of the elytron along the *vena dividens*. The species of *Acosmelytron* and *Parablattelytron* therefore differ in but minor respects that do not warrant generic rank. *Parablattelytron* is the name of this genus by page precedence.

Parablattelytron subincisum Till.

Figure 23C

Parablattelytron subincisum Tillyard, 1931, Amer. Journ. Sci., 21: 251; fig. 10.

Parablattelytron subincisum Carpenter, 1933, Proc. Amer. Acad. Arts Sci., 68: 482.

The unique specimen on which this specimen was based was so poorly preserved that Tillyard was unable to present a satisfactory description of the species. Since some of the new specimens are better preserved than any others that have been collected, the species is redescribed here: Length of elytron, 6.5–7.5 mm.; width, 2–2.3 mm. Costal expansion well developed; sutural margin unusually narrow; Sc well developed proximally and extending almost to the apex of the wing, the distal part being weak; R strongly formed, Rs absent; M weakly formed; Cu1 coalesced with M proximally, very weakly developed and atrophied at about the middle of the wing; *vena dividens* (and possibly Cu2) well developed proximally; portions of two anal veins are exceedingly weakly formed.

Plesiotype: No. 4364ab, Museum of Comparative Zoölogy; collected in the upper layer of limestone by F. M. Carpenter, 1935. This is a specimen of an elytron, better preserved than any other which has been found.

In addition the foregoing specimen, seven other representatives of this species were collected in 1935, all in the upper layer, except the last: 4354ab, 4358–4364.

Parablattelytron rectum Till.

Parablattelytron rectum Tillyard, 1931, Amer. Journ. Sci., 21: 252.

Ten specimens of this species were collected in 1935: Nos. 4346–4353, 4356; all were found in the upper layer except for Nos. 4349–4352. Some of these consist of very well preserved elytra (e.g. No. 4348), which prove that Sc and R were long,

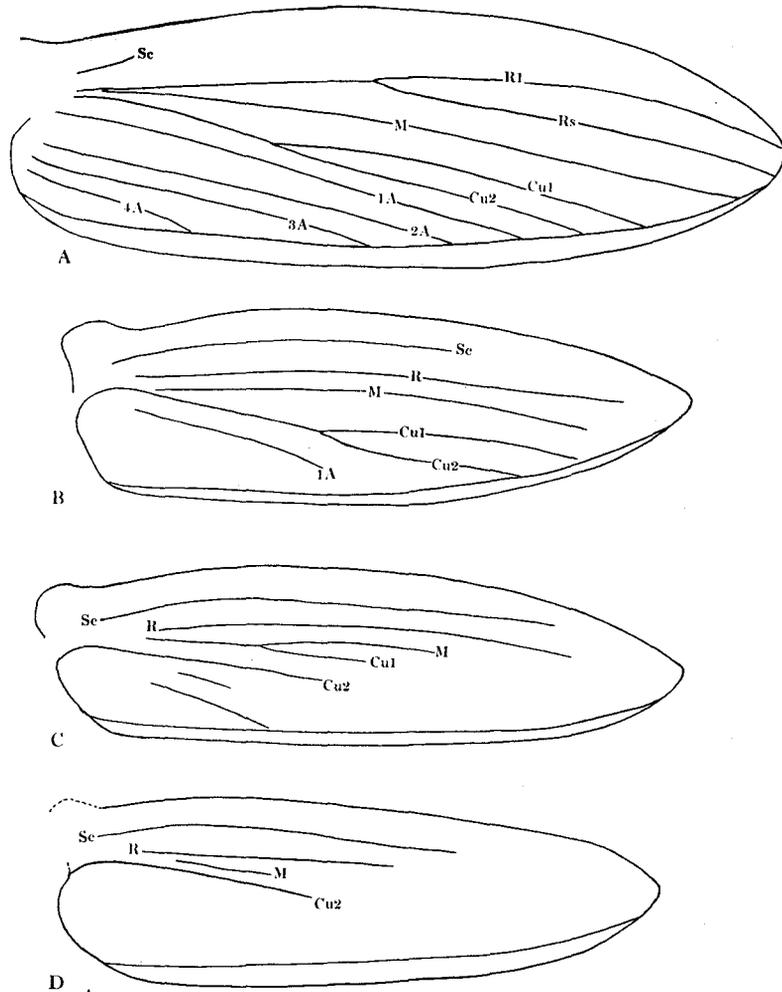


FIGURE 23. A. *Protelytron furcatum*, n. sp., drawing of elytron; holotype, No. 3885ab, Museum of Comparative Zoölogy. B. *Permelytron schucherti* Till., drawing of elytron; No. 4028ab, Museum of Comparative Zoölogy. C. *Parablattelytron subincisum* Till., drawing of elytron; No. 1047, Museum of Comparative Zoölogy. D. *Parablattelytron elongatum* (Till.), drawing of elytron; No. 4365, Museum of Comparative Zoölogy.



FIGURE 24. *Misthodotes obtusus* Till., drawing of tarsus; specimen No. 4388, Museum of Comparative Zoölogy.

as in *subincisum*; but no specimen shows any indication of M or Cu1.

Parablattelytron elongatum (Till.)

Figure 23D

Acosmelytron elongatum Tillyard, 1931, Amer. Journ. Sci., (5) 21: 253; fig. 12.

Acosmelytron elongatum Carpenter, 1933, Proc. Amer. Acad. Arts Sci., 68: 481.

One very finely preserved elytron of this species (No. 4365, lower layer) was found in 1935 (figure 22d). A reexamination of all known specimens of *elongatum* and *subincisum* convinces me that the elytra of these two species differ only in the width of the sutural margin (which is very broad in *elongatum*) and in the more advanced obsolescence of the veins.

Order PLECOPTERA

In addition to numerous fragments, twenty-three fine specimens of may-flies were collected in 1935. Eleven of these are the common species, *Protereisma permianum* Sell. (Nos. 4367-4375, all upper layer except the first). Two of these add to our knowledge of the body structure of this insect. Specimen No. 4373ab, which consists of part of the wings and body, has the prothorax especially well preserved; it shows that this segment was broader and had more indications of the paranotal lobes than has previously been supposed. Specimen No. 4375ab, consisting of part of the body and wings, has one of the legs preserved in lateral view; the tarsus is seen to possess a number of prominent ventral spines, which I have not discerned in previous material.

The following species deserve further comment:

Protereisma insigne Till.

Protereisma insigne Tillyard, 1932, Amer. Journ. Sci., (5) 23: 259; fig. 18.

Since this species, the largest of the genus,²⁰ has previously been known only from the type and another fragment, it is noteworthy that five more specimens were found in 1935, three (Nos. 4379, 4381, 4383) in the lower layer and two (Nos. 4382, 4390) in the upper layer. Both fore

and hind wings are represented in this series, and are seen to differ in the same respects as those of the other species of *Protereisma*. One proximal part of a fore wing (No. 4390), which is especially well preserved, shows Rs arising from the very basal part of M, not coalesced with it for a short distance, as is the case in the other species of the genus.

Family MISTHODOTIDAE

Genus *Misthodotes* Tillyard

Misthodotes obtusus Sell.

Figure 24

Dromeus obtusus Sellards, 1907, Amer. Journ. Sci., (4) 23: 551.

Misthodotes obtusus Tillyard, 1932, *ibid.*, (5) 23: 261.

Six specimens of *Misthodotes* were collected in 1935, two being *ovalis* Till., and the others *obtusum* Sell. Three of the latter are especially interesting (Nos. 4387-4389, all upper layer), since they include portions of the body which have not previously been preserved. Although it has been apparent from material collected earlier that the legs were much shorter than those of the species of *Protereisma*, the details of the legs of *Misthodotes* were not known. The three specimens mentioned show these details very satisfactorily and it is interesting to note their peculiarities in this genus. In *Protereisma permianum*, the body structure of which was apparently typical of that throughout the genus, all the legs were exceedingly elongate, all pairs being from 20-23 mm. in length. In *Misthodotes obtusus*, the fore leg was only 5 mm. long (femur 1.7 mm., tibia 1.5 mm., and tarsus 1.8 mm.), the middle leg 8.5 mm. (femur, 2.5 mm., tibia and tarsus, each 3 mm.), and the hind leg, about 9.5 mm. (femur 3.5 mm., tibia 3.5 mm., tarsus about 2.5 mm.). Unlike *Protereisma*, then, *Misthodotes* had heteronomous legs, the fore pair being considerably shorter than the other two pairs. An even greater difference in the leg structure of the two genera existed in the tarsal segmentation. The tarsi of *Protereisma* were 5-segmented, the penultimate segment being the shortest. The tarsi of *Misthodotes obtusus* (figure 24) however, were but 4-segmented, the two middle segments being very short. This difference in tarsal segmentation should undoubtedly be regarded as another distinction between the two families.

The antennae, which have not previously been known in this genus, are clearly preserved in

²⁰ Tillyard states (1932, p. 259) that this species is the largest known member of the Plecoptera, having a wing length of about 30 mm., but he apparently overlooked the Jurassic *Ephemeropsis trisetalis* Cock., which had a wing length of 35 mm. (Amer. Mus. Novit., 224: 1; 1924).

specimen No. 4389. They are only 1.7 mm. long, much shorter than those of *Protereisma*, but apparently consist of about 15 segments.

Order PROTOPERLARIA

Approximately two hundred specimens of Protoperlaria were collected in 1935, bringing the total number of these insects in the Museum of Comparative Zoölogy to more than eight hundred. In all collections of the Elmo fossil insects combined there are included at least a thousand belonging to this order. Before we come to an account of the new specimens, two general topics need to be clarified. One of these is the definition of the order, and the other is the nature of the characteristics on which its species may be classified.

1. Tillyard originally stated that "the sole criteria of this order are the presence of the lateral, wing-like expansions of the pronotum and the general Perlarian facies, venation and chaetotaxy of the wings." Within this order he placed the single family Lemmatophoridae. In my previous account of these insects (1935) I pointed out that inasmuch as many of the Protorthoptera had similar pronotal expansions and a wing venation very much like that of the Protoperlaria, a more precise definition of the order was needed. Since the structure of their nymphs in the Elmo limestone showed that the immature Protoperlaria were aquatic, I proposed that the order be further defined as including only those orthopteroid insects with pronotal expansions which possessed aquatic nymphs. Also, inasmuch as the adult female of Lemmatophoridae lacked a fully developed ovipositor, I suggested that the presence of such an ovipositor in the true Protorthoptera and its absence in the Protoperlaria be taken as another point of difference between the two orders. In a later paper (1937) Tillyard has added to the order the family Probnisidae Sellards (which had previously been placed in the Protorthoptera by Sellards and in the Miomoptera by Martynov), claiming that he has found aquatic nymphs of *Probnis* in the Yale collection. In this connection Tillyard again considers the definition of the order and appears to take exception to certain of my remarks. He states that the mere absence or presence of an ovipositor in an insect is no indication of the aquatic or terrestrial nature of its nymph. The truth of this assertion is so obvious that I am unable to understand why Tillyard considered it necessary to make it; there is certainly nothing in my paper which

implies that I held any such notion. As a matter of fact I described in detail a very small ovipositor in one of the Lemmatophoridae (*Lecorium*) although as I pointed out this differed greatly from the long, blade-like ovipositor of the related Protorthoptera. My reference to the reduced or perhaps vestigial ovipositor of the Lemmatophoridae was intended only to provide a morphological character serving to distinguish the order Protoperlaria, as it was then known to us, from the related Protorthoptera, which had a fully developed ovipositor. It is obvious from my discussion of this subject, that if the Probnisidae or any related family were found to possess aquatic nymphs, and had a fully developed ovipositor in the adult, I would include the group in the Protoperlaria. Since Tillyard had no opportunity before his sudden death to explain his reasons for this association of nymphs and adults of *Probnis*, further discussion of the position of the Probnisidae will be postponed until after the remainder of the Yale collection has been returned to the Peabody Museum and I have studied the nymphs to which he referred. The account of the protoperlarian nymphs found in 1935 will likewise be given then.

2. The classification of the species belonging to the Protoperlaria (Lemmatophoridae) is not an easy matter. As Tillyard has pointed out, in order to understand the systematics of these insects, one must grasp clearly the marked tendency of the venation to vary in individuals. In his account of these insects, Tillyard indicated clearly, by illustrations and tables, the nature and extent of this variation. From his study of 210 specimens in the Yale collection, he was able to distinguish only five genera and nine species within the Lemmatophoridae. My examination of about 600 more specimens of the family substantiated Tillyard's conclusions on the variability of the venation and the number of species represented.

In a recent publication (1937), consisting mainly of a review of the literature on Palaeozoic insects between the years 1920 and 1930, Handlirsch has attempted to revise the classification of the Lemmatophoridae on the basis of the descriptions, illustrations, and tables contained in Tillyard's papers—without, of course, seeing any of the fossils themselves. In this publication Handlirsch erected two new genera and twenty-five new species of Lemmatophoridae in the Elmo limestone; and at the same time reestablished all of Sellards' genera and species, most of which had

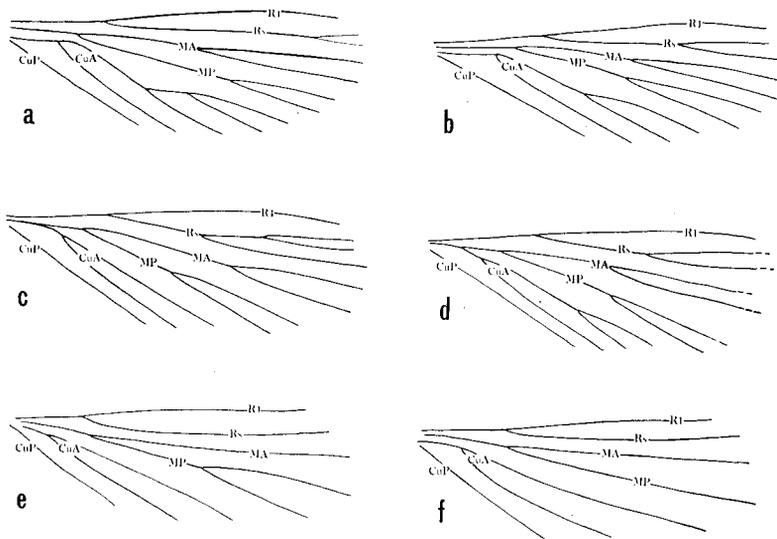


FIGURE 25. Variation of venation in Lemmatophoridae. a, b, left and right fore wings of *Artinska clara* Sell., specimen No. 4455; c, d, same of *A. clara*, No. 4442; e, f, same of *Lisca minuta* Sell., No. 3551. (See also figure 8, Carpenter, 1935).

been synonymized by Tillyard.²¹ It is readily apparent that in his treatment of these fossils Handlirsch did not grasp the variability of the venation of these insects so clearly demonstrated by Tillyard. Thus, he separates the genera of the family, first, on whether or not Cu and M are joined proximally, then, on whether Rs and M are free or coalesced, and finally whether Rs is simple or forked. These, however, are precisely the venational features which are most subject to variation in these insects. Certain proof of their individual variation is provided by those specimens which possess both fore wings. Unfortunately almost no specimens of this sort were contained in the Yale collection and Tillyard was unable to demonstrate the differences in the venation between the left and right wings of individuals. A number of such specimens are in the Harvard collection, however. The fore wings of one of these (*Lecorium elongatum* Sell.) has already been figured in my previous account of the *Protopeplaria* (1935, fig. 8), and drawings

²¹ To a certain extent, Tillyard may have misled Handlirsch by his use of the word "variety" for a number of individuals which showed venational peculiarities not previously mentioned by Sellards. In no case, however, did he actually name these so-called varieties, and it is at once clear that he did not use the term as indication of a trinomial nomenclature. It seems to me that the policy of naming varieties (trinominals) of fossil insects, known from wings or wing fragments, is entirely meaningless.

of the venation of some of the other specimens are included here (figure 25). The specimens which have been illustrated are not unique in regard to the degree of differences in venation, but have been selected because they show the variability of the characteristics used by Handlirsch in his generic and specific classification of these insects. An attempt to determine these specimens on the characteristics used by Handlirsch shows that one wing of a specimen belongs to one of his genera or species, whereas the other wing belongs to another genus or species. Certainly, since the right and left wings of individuals exhibit such differences as these, we can only conclude that at least as great a variation takes place in the wings of different individuals, especially inasmuch as none of the hundreds of isolated wings which have been found are alike in these respects, and all show various degrees of intergradations. It is perfectly clear, therefore, that none of Handlirsch's new genera and twenty-five new species are valid. The synonymy of these is indicated in the list of species given below.

The *Protopeplaria* contained in the 1935 collection are as follows:

Family LEMMATOPHORIDAE

Subfamily LEMMATOPHORINAE

Lemmatophora typa Sellards

Lemmatophora typa Sell., 1909, Amer. Journ. Sci., (4) 27: 162.

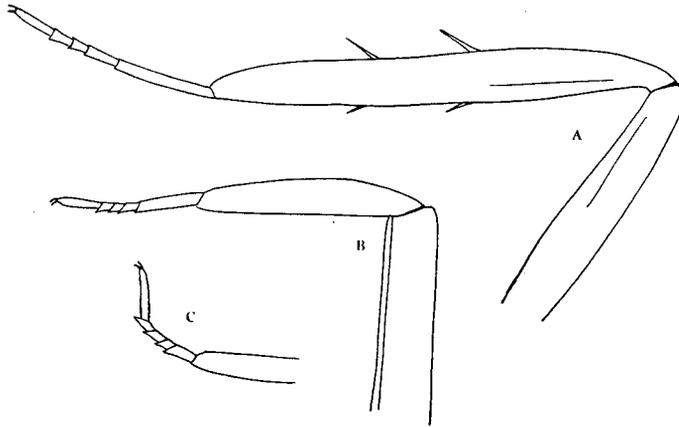


FIGURE 26. *Artinska clara* Till., drawing of legs; A, hind leg (No. 4444); B, middle leg (No. 4456); C, fore leg (No. 4456).

Eighty specimens of this species were collected in 1935, of which thirty are from the lower layer. This increases the total number of known specimens of this species to very nearly four hundred. Although some of these are fairly complete insects (e.g., no. 4426ab), none of them add to our knowledge of the structure of this common species.

Lisca minuta Sell.

Lisca minuta Sellards, 1909, Amer. Journ. Sci., (4) 26: 163.

Lemmatophora cubitalis Handlirsch, 1937, Ann. Nat. Mus. Wien, 48: 93.

Eighty-five specimens were collected in 1935, all but fourteen of which are from the upper layer. Some of these are excellently preserved, showing nearly the complete body (e.g. Nos. 4430-4433); but the structure of this insect is already well known.

Artinska clara Sell.

Artinska clara Sellards, 1909, Amer. Journ. Sci., (4) 26: 165.

Artinska inversa + *pentamera* + *tillyardi* + *nova* + *simplex* + *altera* + *maculipennis* + *reducta* + *kansasia* + *aucta* + *banneria* + *confusa* + *quadrifida* Handlirsch, 1937, Ann. Nat. Mus. Wien, 48: 95.

Fifty-four specimens of this species were collected in 1935, of which twenty came from the lower layer of the limestone. Several of these specimens are better preserved than any which have previously been found, and show body structures previously unknown, such as fore and middle legs. All of the following fossils consist of both wings and portions of the body: Nos. 4436, 4437, 4438, 4439, 4440, 4442, 4443, 4444, 4446,

4449, 4450, 4455 and 4456. The fore leg (fig. 26) which is well preserved in specimens No. 4455 and 4456 is much shorter than the other legs; the tibia is only 1.5 mm. long, and the tarsus but 1 mm. The first four tarsal segments are very short, and almost equal in length, the first being very slightly longer than the others; the fifth segment is equal in length to the previous three combined. The middle leg (fig. 26; specimens No. 4444, 4436) is at least 6 mm. long; the femur as preserved is 2.5 mm. in length, and the proximal part is not preserved; the tibia is 2 mm. and the tarsus is 1.5 mm. The first tarsal segment is greater in length than the next three combined, which are short and equal, the last segment is nearly as long as the first. The hind leg of *A. clara* (fig. 26) has already been described (Carpenter, 1935, p. 120), and it is interesting to note that the structure of the hind legs of the new specimens (No. 4456, 4444, 4455) agrees in all details with that of the earlier fossil. This leg is better preserved in the 1935 specimens however, and shows several large tibial spines not previously observed in *Artinska*, though they have been found in *Lemmatophora typa*.

Specimen No. 4456 is of special interest because it is a laterally preserved insect and shows abdominal appendages which are like those of *Lecorium* and which appear to represent a reduced or vestigial ovipositor.

Artinska ovata Sell.

Artinska ovata Sellards, 1909, Amer. Journ. Sci., (4) 26: 168.

Orta tillyardiana + *sellardsiana* + *reducta* Handlirsch, 1937, Ann. Nat. Hist. Mus. Wien, 48: 96.

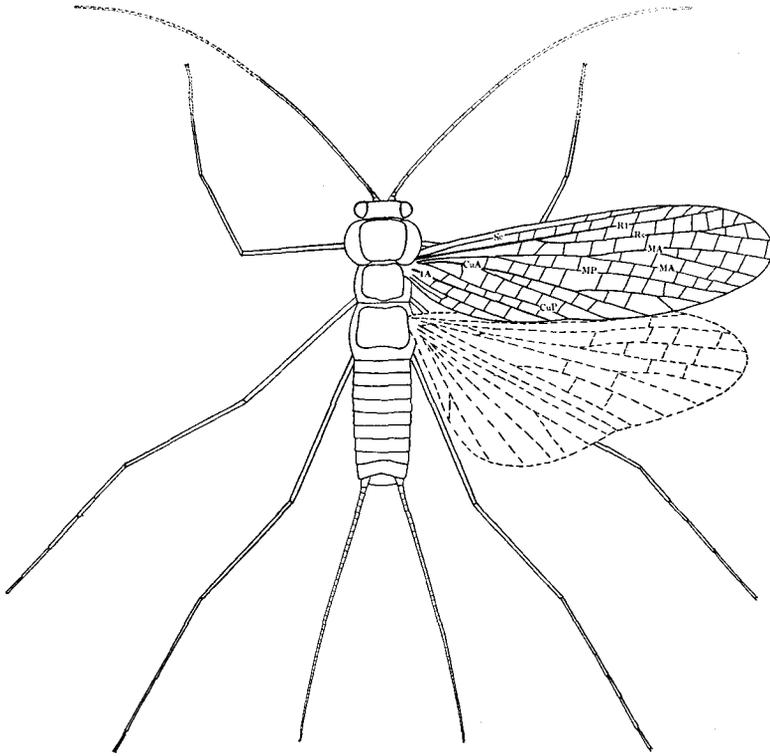


FIGURE 27. *Paraprisca grandis* Carp., reconstruction, based on specimens numbered 4457ab, 4451ab, Museum of Comparative Zoölogy.

Only twenty specimens of this species were collected in 1935, half of which came from the lower layer. This is consistent with my previous suggestion that *ovata* is much less common in the upper layer of the limestone than in the lower, for most of the collecting in 1935 was done in the upper layer. Some of these fossils show the general form of the body, and one (No. 4448) includes the cerci and a hind wing, neither of which have previously been found. The cerci are 2.5 mm. long. The venation of the hind wing is like that of *clara*: Rs is forked, MA is unbranched, MP is forked, and CuA has the fork characteristic of the family.

It should be noted in passing that the wing venation of the specimen illustrated in my previous account of the *Protoperlaria* (1935, fig. 4) is not entirely typical of the species in the form of the radius. There is usually not quite so much curvature at the origin and at the distal part of Rs.

Subfamily PARAPRISCINAE

Paraprisca fragilis Sell.

Paraprisca fragilis Sellards, 1909, Amer. Journ. Sci., (4) 26: 167.

Lemmatophora longipennis Handlirsch, 1937, Ann. Nat. Hist. Mus Wien, 48: 93.

Twelve specimens of this curious insect were collected in 1935; seven of these are from the upper layer and these constitute the first specimens of the species taken in that level of the limestone. None of these show any portions of the body that have not already been described; the structure of the fore and middle tarsi is still unknown.

Paraprisca grandis Carp.

Figure 27

Paraprisca grandis Carpenter, 1935, Proc. Amer. Acad. Arts Sci., 70: 128, fig. 6.

Paraprisca grandis Tillyard, 1937, Amer. Journ. Sci., 33: 97.

Paraprisca stigmatica Tillyard, 1937, *ibid.*, p. 97, fig. 5.

Four specimens of this rare species were collected in 1935, all in the upper layer of the limestone. Two of these (Nos. 4457, 4451) are very nearly complete specimens and show much of the body structure, which has not previously been known at all.

As Tillyard pointed out, certain of the veins were incorrectly labelled in my original figure of this species, although the description of the venation was accurate. The vein marked CuP is 1A, CuA3 is CuP and CuA2 is CuA3. The correct labelling is shown in figure 27 of the present paper.

The new fossils show that some modification of our conception of this species is needed. In the type specimen, Sc was considerably shorter than it seemed to be in *fragilis* and CuA had an unusual mode of forking. The new specimens of *fragilis*, however, show a variation in the length of Sc not previously noted, and the new *grandis* also demonstrates a similar variation in the length of this vein. Similarly, the forking of CuA is not the same in any two specimens of *grandis*, so it is apparent that this species is just as variable in venation as the other members of the family Lemmatophoridae. The two species, *fragilis* and *grandis*, do not apparently have any venational differences which are constant enough to separate them. That two species are represented is, however, unquestionable, *grandis* being nearly twice the size of *fragilis*, and the body structure being decidedly different, as shown below.

Tillyard's *stigmatica* is without doubt a synonym of *grandis*, in my opinion. The size of the wing (14 mm.) falls within the range of that of *grandis* (14–18 mm.). Tillyard separated the species from *grandis* on the basis of a different form of fork on CuA, and the presence of a pterostigma. The useless nature of the forking of CuA as the source of specific characteristics has already been mentioned; there are no two specimens of *grandis* which are alike in the form of CuA and the variations range all the way from that of the type of *grandis* to that of the type of *stigmatica*. In regarding the presence of the pterostigma as specific in nature, Tillyard has overlooked the differences in the appearances of the wings when they are preserved. It should be noted that the pterostigma of this *stigmatica* is not a thickened area of the wing, but is merely indicated by the presence of a patch of brown pigment. The paratype of *grandis* consists of a wing which is slightly brownish over its entire surface but a slight darkening of the area is present in the pterostigmal area, and along the whole of R1, as described by Tillyard in *stigmatica*. The holotype of *grandis* and the other specimens of the species have colorless wings, which is in accordance with my previous remarks on the individual

variation of the coloration of the Kansas fossils. I am therefore led to conclude that, inasmuch as there are no valid venational differences between *stigmatica* and *grandis*, the specimens of the former are simply those which during preservation have lost all the wing coloring except that of the pterostigmal area and the region of R1.

The body structure of *P. grandis* is so well preserved in the two specimens already mentioned that we are able to form an even better idea of the general habitus of this insect than we are of *fragilis*. As in the latter, the legs of *grandis* are long and slender, but their tenuity is carried to a remarkable extent (figure 27). Both of the specimens which show the body structure are approximately the same size, and the dimensions of the appendages are very nearly identical in both fossils. The body, including the cerci, is 25 mm. long, the cerci being 12 mm. These are much larger figures than in the case of *fragilis*, with a body 5 mm. long and cerci 1.5 mm. long. The antennae are preserved to only a length of 6 mm. in one specimen of *grandis* and 7 mm. in the other; in view of the long antennae in *fragilis*, I presume that those of *grandis* are probably at least 16 mm. in length. The preserved antennal segments of *grandis*, however, are proportionally twice as long as those of *fragilis*.

The head is well preserved in only one specimen (No. 4451). The eyes are much larger and more bulging than those of the other Protoperlaria, if our interpretation of the head structure of the other species is correct. The thoracic segments and the nota are typical of those of the Lemmatophoridae; the thorax as a whole is 6 mm. long. The paranotal lobes are very small, but are nevertheless distinct. The abdomen, which is 5 mm. long, possesses the lateral gill vestiges characteristic of the family. The cerci are extraordinarily long, very nearly equally the length of the whole body proper, and including about fifty segments. The legs of *grandis* are truly astonishing. Even the fore pair are at least 12 mm. long, and the middle and hind pairs are 21 mm. in length. Proportionally, therefore, the legs of *grandis* are even more elongate than those of *fragilis*. The dimensions of the leg segments are as follows: *fore leg*, femur, 5 mm.; tibia, 4 mm.; tarsus, at least 3 mm. (incomplete); *middle leg* and *hind leg*, femur, 7 mm.; tibia 6 mm.; tarsus 8 mm. The tarsus of the fore leg is not completely preserved and its segments are not clear. Only the first two tarsal segments of the middle leg are preserved; the first is about twice as long

as the second. The first two and the last of the hind tarsal segments are clear; the first is about three times as long as the second and twice as long as the last.

In figure 27 I have presented a restoration of this insect, based on the two specimens indicated. Those parts represented by broken lines are purely hypothetical, since they are not preserved in the fossils. The hind wing is not known at all, but I have added the hind wing of *fragilis* in order to give as completely as possible the general habitus of the insect; in all probability the hind wing of *grandis* does not differ materially from that of the genotype (*fragilis*).

Genus *Lecorium* Sell.

Lecorium Sellards, 1909, Amer. Journ. Sci., (4) 26: 167.

Paralecorium Handlirsch, 1937, Ann. Nat. Musm. Wien, 48: 96.

Metalecorium Handlirsch, 1937, *ibid.*, p. 96.

Lecorium elongatum Sell.

Lecorium elongatum Sellards, 1909, Amer. Journ. Sci., (4) 26: 167.

Paralecorium parvum + *Metalecorium confusum* + *Sellardsia separanda* + *S. abnormis* Handlirsch, 1937, Ann. Nat. Hist. Mus. Wien, 48: 97.

Twelve specimens of this insect were collected in 1935, eight from the lower layer. This small number is undoubtedly due to the scarcity of this insect in the upper layer. None of these fossils show structures not already described. Handlirsch's new genera and species were erected on the differences of the forking of the media; the facts pointing to the synonymy of these will be found in my earlier account of the venation of this genus (Carpenter, 1935, p. 133-134).

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EXPLANATION OF PLATES

PLATE 1

Figure 1. Photograph of part of the 1935 Harvard quarry at Elmo, Kansas, showing the thinning of the Elmo limestone at the east edge of the quarry (left of the photograph). a, upper layer of limestone; b, lower layer.

Figure 2. Photograph of the same part of the quarry, facing east.

Figure 3. *Permoscytina kansasensis* Till. Photograph of specimen No. 3811, Museum of Comparative Zoölogy; dorsal view, showing head (a), part of fore leg (b), and long abdominal process (respiratory tube). The wings of this specimen are illustrated in text figure 17. Length of fore wing, about 11 mm.

PLATE 2

Figure 1. *Archescytina permiana* Till. Photograph of holotype, No. 5111b, Peabody Museum, showing absence of independent subcosta (cf. Tillyard, 1926c, fig. 4). Length of wing, 7 mm.

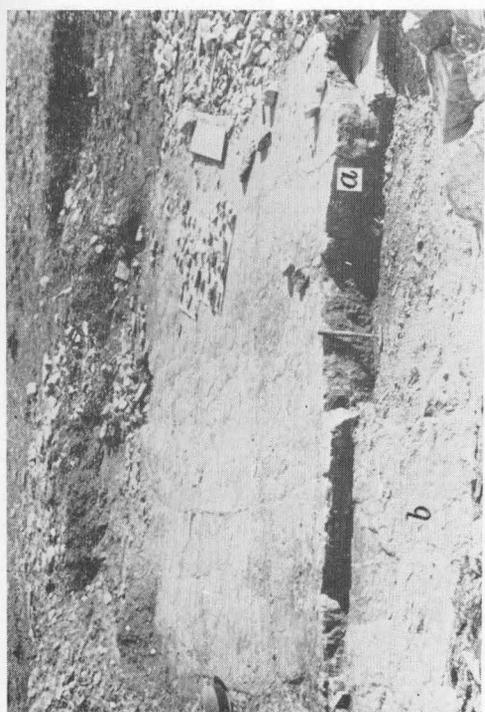
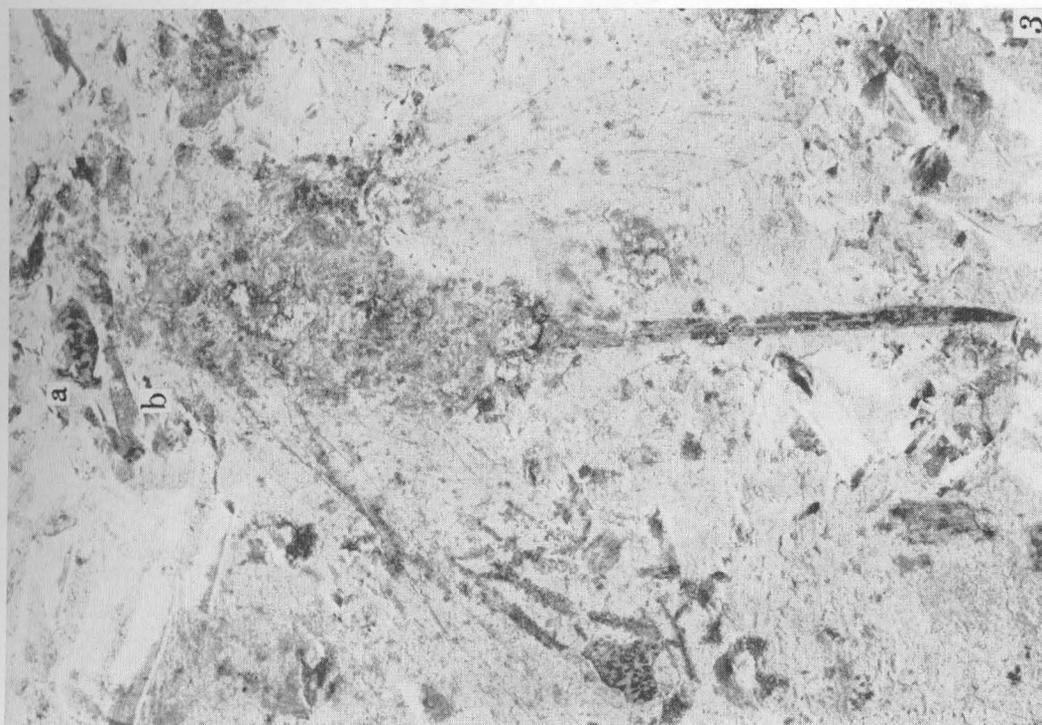
Figure 2. *Asthenohymen dunbari* Till. Photograph of specimen No. 3822, Museum of Comparative Zoölogy; lateral view, showing head and complete cerci. Length of fore wing, 6 mm.

Figure 3. *Delopteryx minutum* Sell. Photograph of specimen No. 3979, Museum of Comparative Zoölogy; dorsal view, showing short cerci. Length of fore wing, 4.5 mm.

Figure 4. *Permohymen schucherti* Till. Photograph of terminal part of abdomen, specimen No. 3979, Museum of Comparative Zoölogy. Length of part shown in photograph, 2.5 mm.

Figure 5. *Permopsocus latipennis* Till. Photograph of body, specimen No. 3992, Museum of Comparative Zoölogy, showing terminal abdominal processes (copulatory hooks?). Length of process, 1 mm.

Figure 6. *Dichentomum tinctum* Till. Photograph of end of abdomen, specimen No. 4016, Museum of Comparative Zoölogy, showing copulatory hooks. Length of hooks, .6 mm.



1

2

