

THE LOWER PERMIAN INSECTS OF KANSAS. PART 12.
PROTORTHOPTERA (CONTINUED), NEUROPTERA,
ADDITIONAL PALAEODICTYOPTERA, AND
FAMILIES OF UNCERTAIN POSITION¹

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The three preceding parts in this series have dealt with families of Protorthoptera and Orthoptera occurring in the insect beds in Elmo, Kansas. The present paper includes a few other families of Protorthoptera, the first family of the Order Neuroptera, a new family of Palaeodictyoptera, and a series of five families that I have been unable to assign to any known order. Most of these fossils were collected in the Harvard quarry in 1927 and during the intervening fifty years I have studied them many times over in attempts to determine their relationships. It now seems advisable to describe them formally, even though some uncertainties still exist.

ORDER PROTORTHOPTERA

As our knowledge of Permian insects increases, it becomes obvious that orthopteroids were the predominant types of insects during the entire period. The Blattaria and Miomoptera were abundant as individuals and probably also as species; the Protelytroptera and Orthoptera, although not so numerous, represent very different structural and environmental divergences. The rest of the Permian orthopteroids (apart from the enigmatic Caloneurodeia) have been referred to the Order Protorthoptera — a very large, complex, and probably polyphyletic taxon (See Carpenter, 1966). It is here that the maximum diversity is found. In the Elmo

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beds alone eleven families of Protorthoptera have already been recognized, these being the following: Blattinopsidae, Strephocladidae, Stereopteridae, Tococladidae, Liomopteridae, Demopteridae, Phenopteridae, Protelmiidae, Probnisidae, and Lemmatophoridae. Three additional families are described below.

Family **Nugonioneuridae**, new family

Insects of moderate size, with a wing expanse of about 20 mm. Fore wing: SC terminating on R1; RS arising at about mid-wing; stem of M coalesced basally with CUA, the branches of M arising abruptly from M+CUA and arching anteriorly; several anal veins present. Cross veins numerous and irregularly distributed, mostly unbranched and not forming a reticulation. The hind wing, not certainly known, is discussed below in the account of *Nugonioneura problematica*. Body unknown.

At present only the type genus is known in the family.

Genus *Nugonioneura* Tillyard

Nugonioneura Tillyard, 1937, p. 92.

Fore wing: costal margin with a small bulge basally; SC terminating on R1 just beyond the origin of RS; costal area with several oblique cross veins and the area between R1 and costal margin with several to many cross veins; RS with from 2 to 4 terminal branches; M+CUA with from 4 to 6 primary branches; CUP nearly straight, the area between M+CUA and CUP being broad; at least 4 anal veins present. Cross veins mostly straight, some oblique; wing membrane granular.

Type-species: *Nugonioneura problematica* Tillyard

Nugonioneura problematica Tillyard

Figures 1-3

Nugonioneura problematica Tillyard, 1937, p. 94, fig. 4

Fore wing: length 9.5-12 mm; width, 3-3.5 mm. Costal margin convex but with a slight concavity or straight portion near mid-wing; subcosta somewhat irregular in form, apparently with a few

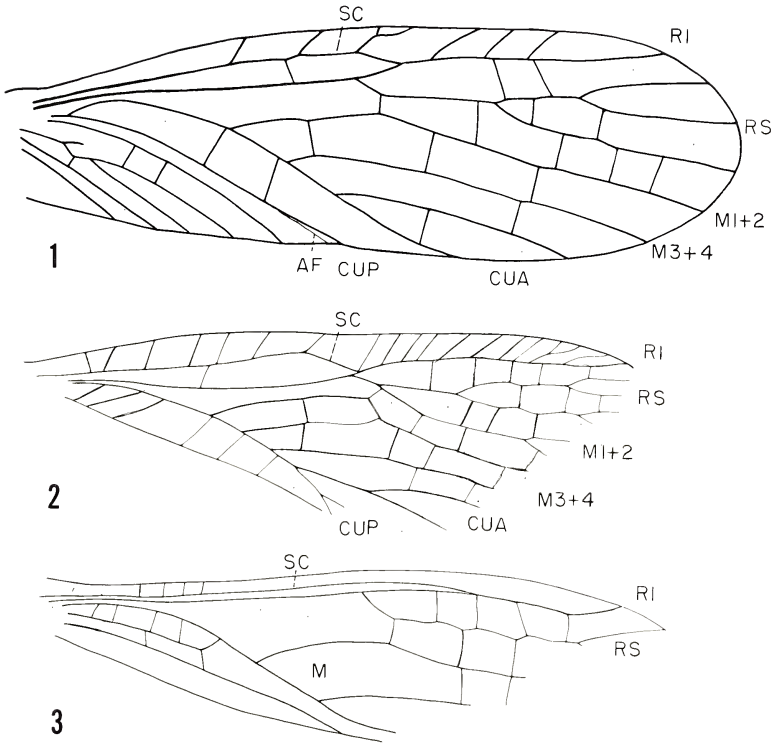
to several cross veins in the costal area; branching of RS variable; in some specimens R2+3 and R4+5 are forked but in others they are simple; branching of M+CUA also variable.² CUP is close to 1A and appears to follow the anal fold for most of its length.

Holotype: no. 15561, Peabody Museum, Yale University. As shown in Tillyard's figure, this consists of a poorly and incompletely preserved fore wing, lacking the posterior region and having most of the veins faintly preserved. I have carefully studied this specimen and I find no clear evidence that R1 is forked, as shown in Tillyard's figure; the anterior veinlet shown is almost certainly one of the several cross veins in that area. Also, M+CUA does not coalesce with RS as figured by him; there may be a short connection between these two veins, though it is not visible in any specimen.

Two additional fore wings of *problematica* are now at hand and have been used in part as the basis of the foregoing description of the genus and species. One of these, no. 5895ab, Museum of Comparative Zoology, consists of a complete and very well preserved fore wing (figure 1). It is the same size as the type and differs only in the number of branches of RS and M: R2+3 is deeply forked and there is one less terminal branch of M. However, these are the kinds of variations that usually occur within species of orthopteroids (see Carpenter, 1966). It should also be noted that in this fossil CUA is directed distally at its termination, away from CUP, not towards CUP; this is probably correlated with the absence of the terminal fork on CUA. The anal area is not sharply marked off, except for the slight indentation of the hind margin at the end of CUP. The cross veins are only faintly preserved in this fossil; in the accompanying figure only those that can positively be discerned are shown; others may be present, as indicated in the other specimens of this insect.

The second new specimen consists of an incomplete wing, no. YPM 27536, Peabody Museum, Yale University (figure 2). It is slightly larger than the other two specimens, with a length of 12 mm and width of 3.5 mm. The differences between this specimen

²It is not possible to distinguish between the branches of these two veins (M and CUA), since they do not show convexities or concavities. I have arbitrarily assumed that the last fork of M+CUA comprises CUA, and the other branches, M.



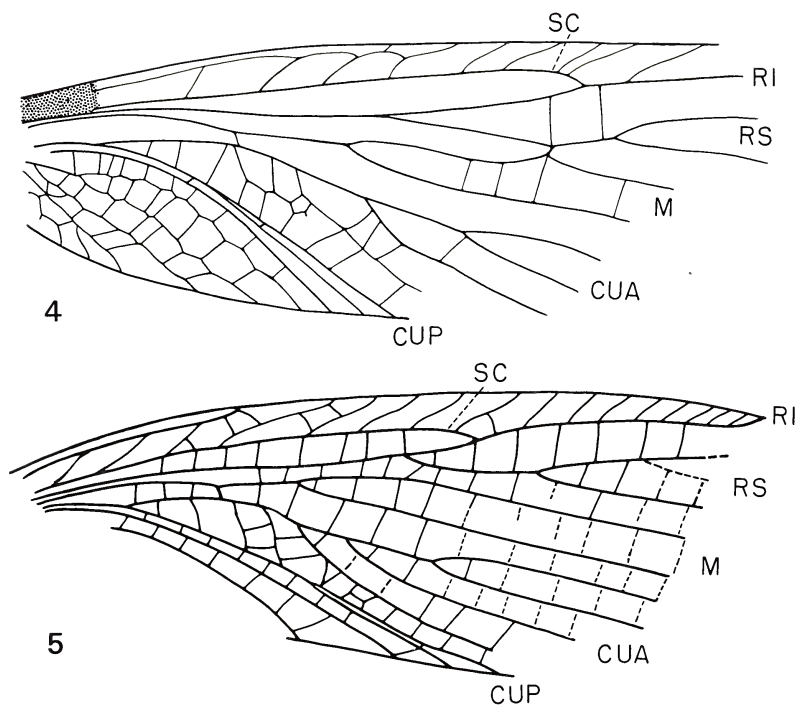
Figures 1-3. *Nugonioneura*. Fig. 1, *N. problematica*; drawing of fore wing, based on specimen no. 5895, M.C.Z. Length of wing, 10 mm. Fig. 2, *N. problematica*; drawing of fore wing, based on specimen no. YPM27536, Peabody Museum, Yale University. Length of wing, 10 mm. Fig. 3, *N. problematica* (identification uncertain); drawing of hind wing, based on specimen no. 7504, M.C.Z. Length of wing, 10 mm. AF, anal fold. The terminology of the wing veins used in all parts of this series of papers is discussed in Part 11 (Carpenter 1966).

and the others are mainly in the branching of RS and M: RS has 4 terminal branches and there are 5 terminal branches of M arising from M+CUA, as in the holotype. The cross vein between M and RS, near the origin of the latter, is very short, but this is undoubtedly an individual variation.

I see no reason to doubt that these three specimens are fore wings of one species. There is also another specimen in the Har-

vard collection which is probably this insect (no. 7504, Museum of Comparative Zoology). It is an incomplete wing, having the basic venational pattern of *problematica* but the costal and subcostal areas are very narrow. This is a feature of hind wings, at least of orthopteroid insects, and I am of the opinion that this fossil is the hind wing of *problematica*. As shown in figure 3, the costal space has the small bulge basally, as in the fore wing; SC terminates on R1 just beyond the origin of RS, which has a single fork; M+CUA gives rise to two arched branches of M; CUP is widely separated from CUA and there is a short vein, apparently formed by the alignment of cross veins in that space; IA is remote from CUP, unlike the structure of the fore wing. The wing is not preserved beyond IA but there is an indication that the rest of the anal area is folded back under the wing proper, an oblique line apparently marking the inner margin of the wing.

The type specimen of *Nugonioneura problematica* was one of the "puzzles" that Tillyard found in the Yale collection of insects from Elmo. He believed that it had a combination of characteristics of the Psocoptera, Hemiptera (Homoptera), Embioptera, and Protorthoptera, and finally placed it in the family Permembidae of the Order Psocoptera. *Permembia* itself, however, was and still is another puzzle; as noted below, it cannot even now be assigned with confidence to any known order. Our knowledge of *Nugonioneura* has been much improved since Tillyard's description of it, and in addition we have a much better idea of the extraordinary diversity of the Protorthoptera during the Permian than previously. Within that complex aggregation of insects, we can distinguish species suggestive of Psocoptera, Hemiptera (Homoptera), Miomoptera, Perlaria, and of course several existing orthopteroid orders. However, these possible relationships are indicated mainly by the fore wing venation, little being known about the body structure of the Protorthoptera and even less about their hind wings. In my opinion, therefore, it is futile to attempt at this time to trace the evolutionary lines within the Protorthoptera apparently leading to certain existing orders. Even less justified, I believe, is the assignment of such poorly-known fossils to the existing orders concerned. For this reason, I have placed the *Nugonioneuridae* in the Order Protorthoptera. As a member of that order, it is distinguished from other families by the coalescence of M with



Figures 4 and 5. *Opisthocladus*. Fig. 4, *O. arcuatus*, n.sp.; drawing of fore wing, based on holotype, no. 5882ab, M.C.Z. Length of wing as preserved, 13 mm. Fig. 5, *O. strictus*, n.sp.; composite drawing of fore wing, based on both wings of holotype. Length of wing as preserved, 7 mm.

CUA for most of their lengths and by the branches of M arching abruptly from M+CUA before mid-wing. No close relatives are known.

Family Tococlididae Carpenter

Tococlididae Carpenter, 1966, p.76.

This family was designated for a single genus and species, *Toco-cladus rallus* Carpenter (1966) from Elmo. Two other species, representing a new genus, are described below. One of these, *Opisthocladus strictus*, is of particular interest since it is based on a specimen that shows some details of the body structure, which has not previously been known in this group of Protorthoptera.

Opisthocladus, new genus

Fore wing: slender, apparently much as in *Tococladus*. Costal area of moderate width, its basal portion thickened and heavily sclerotized; SC ending on R1 beyond mid-wing and giving rise to several strong cross veins, some of which are at least slightly sigmoidal or which may be looped together, forming an irregular submarginal vein; oblique cross veins extend from R1 to the costal margin beyond SC; RS arising well before the end of SC, connected to or possibly coalesced with M1+2 for a short distance; M arising independently from wing base; CU forking close to wing base into CUA and CUP; CUA forming 3 or 4 long branches; CUP remote from CUA, the broad space between having several cross veins that form at least a few large cells; CUP rests in the anal fold basally, but diverges from it distally; IA very close to CUP; several other well developed anal veins. Cross veins probably as numerous as in *Tococladus*. Hind wing unknown. Body structure: head relatively large, with prominent eyes, dentate mandibles; thorax large, the segments very distinct; abdomen short, as preserved, apparently compressed; cerci unknown.

Type species: *Opisthocladus arcuatus*, n.sp.

This genus differs from *Tococladus* by having looped costal veinlets, the late origin of RS, and the longer and straighter basal portion of CUA. RS almost certainly has fewer branches than in *Tococladus*, but that is not definite, since the apical part of the wing is not preserved. The basal portion of the costal area is heavily sclerotized in *Opisthocladus*; this may have been the case in *Tococladus* also, since the basal part of the wing is unknown in that genus.

The generic name is derived from the classical Greek words *opistho-* (hinder) and *klados* (branch), and is considered masculine and singular.

Opisthocladus arcuatus, n.sp.

Figure 4

Fore wing: length (as preserved), 13 mm; width, 4.5 mm; estimated complete length (based on proportions of *Tococladus ralus*), 17 mm. Costal veinlets mostly oblique and sigmoidal; M forking just before origin of RS; CUA connected to M by a short,

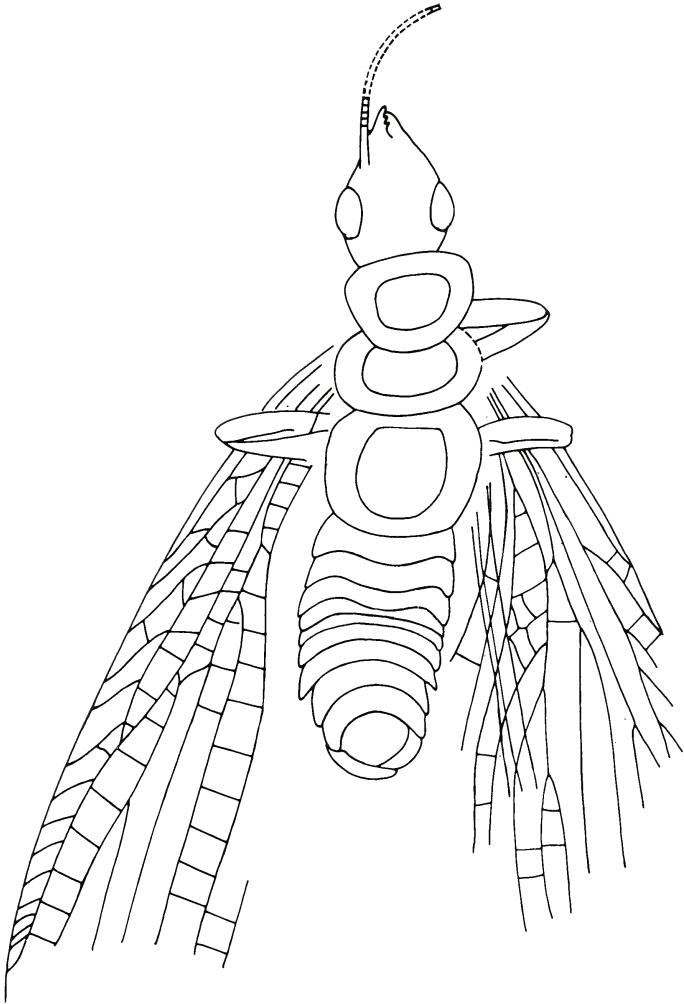


Figure 6. *Opisthocladus strictus*, n.sp.; drawing of holotype, no. 5881ab, M.C.Z. Length of body, 13 mm.

thick cross vein; several of the cross veins between CUA and CUP forming a few large, closed cells; 2A with two deep forks.

Holotype: no. 5882, Museum of Comparative Zoology. This consists of a single fore wing, lacking about the apical quarter; the preserved portion is very clear. Whether M1+2 is actually coalesced with RS or only connected to it by a cross vein cannot be determined in the type specimen; in either case, the nature of the connection is probably subject to much individual variation, as in most other Protorthoptera.

Opisthocladus strictus, n.sp.

Figures 5 and 6

Fore wing: length (as preserved), 13 mm; estimated complete length (based on *Tococladus*), 15 mm. Costal veinlets near the base strongly sigmoidal and forming a short submarginal vein; other costal cross veins nearly straight and not looped; SC terminating on R1 at about mid-wing, only a short distance beyond the origin of RS; M and CU much as in *arcuatus*, but cross veins more definite.

Holotype: no. 5881, Museum of Comparative Zoology. This consists of a complete insect showing a dorsal-ventral view of the body, with the fore and hind wings over-lapped on each side (figure 6). Although the preservation is excellent, parts of the fore wings and virtually all of the hind wings are obscured. Figure 5 is a composite drawing of the fore wing venation based on both of the wings. The body is 13 mm long, from the tip of the mandibles to the end of the abdomen; the head is 2.5 mm long. Only fragments of the antennae are preserved; they indicate a very slender antenna, of at least moderate length. The head, seen in dorsal view (probably distorted into an abnormal, prognathous position), shows the mandibles clearly; they are relatively long and dentate. The eyes are prominent. The thoracic nota are distinct, the segments apparently not fused, and the metathorax is the largest. Little can be seen of the legs; the abdomen, as preserved, is very short, most of the segments apparently being contracted. Terminal structures on the abdomen, including cerci, cannot be discerned.

This species differs from *arcuatus* in lacking the looped costal veinlets, and in having the origin of RS closer to the end of SC

and M forked near the wing-base.

Family **Psoropteridae**, new family

Small insects. Fore wing: costal area narrow. Stem of M fused with stem of CU at base and then for a greater distance with CUA; RS unbranched; M with two branches, CUA with three; CUP unbranched; two anal veins. Longitudinal veins unusually thick and heavy but cross veins weak and thin. Wing membrane uniformly rugose, without hairs. Hind wing and body unknown.

Psoroptera, new genus

Fore wing: RS extending nearly to wing apex, unbranched; RS arising well before mid-wing; M+CUA about as long as the rest of M before its forking into M1+2 and M3+4; CUA diverging from M just before the level of the origin of RS, and forking just beyond that point; M1+2 coalesced with RS for as long an interval as the free piece of M; CUA forming three strong branches, the first arising just beyond the level of the origin of RS.

Type-species: *Psoroptera cubitalia*, n.sp.

The generic name is derived from the classical Greek words *psoro-* (scabby) and *ptera* (wings) and is considered neuter plural.

Psoroptera cubitalia, n.sp.

Figure 7

Fore wing: length, 6 mm; width, 1.8 mm. M1+2 and M3+4 un-

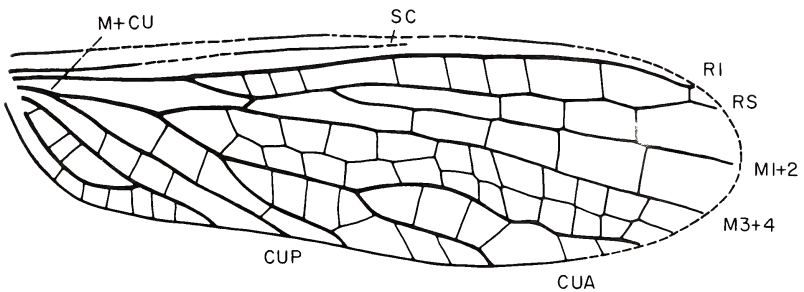


Figure 7. *Psoroptera cubitalia*, n.sp.; drawing of fore wing, based on holotype, no. 5840, M.C.Z. Length of wing, 6 mm.

branched; cross veins between M3+4 and CUA forming an irregular, double row of cells; 2A looped to 1A distally.

Holotype: no. 5840, Museum of Comparative Zoology. This specimen consists of a well preserved fore wing, complete except for small parts of the fore margin and the very apex.

Until a more nearly complete specimen is found, showing at least the hind wing, the affinities of this family will probably remain uncertain. In general, it seems protorthopterous, though the basal fusion of M with CU and CUA, the very heavy longitudinal veins, weak cross veins, and rugose membrane set it apart from all other families of Protorthoptera known to me.

Family **Heteroptilidae**, new family

Insects of moderate size. Fore wing: membranous; costal margin strongly convex; costal area very broad, broadest near mid-wing, with many straight, oblique and unbranched cross veins; subcostal area broad, with straight cross veins; R curved away from the costal margin; R1 strong, directed anteriorly and terminating on costal margin well before wing apex; RS arising before mid-wing, with several branches; M independent of R basally, forking beyond origin of RS; CU forked near base; CUA mostly straight; CUP very straight, extending to about half the wing length; 3 straight anal veins. Cross veins generally weakly developed and not numerous, except in costal area. Hind wing and body unknown.

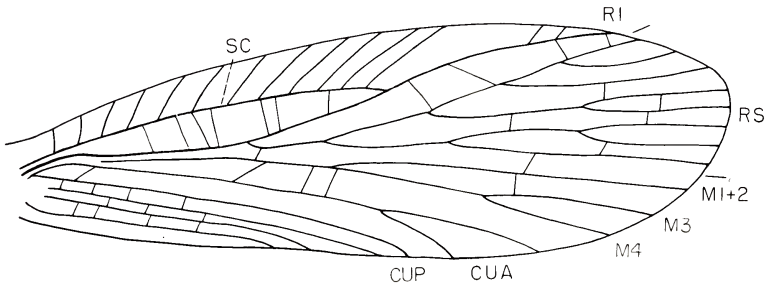


Figure 8. *Heteroptilon costale*, n.sp.; drawing of fore wing, based on holotype, no. 5878, M.C.Z. Length of wing, 15 mm.

This distinctive family is characterized by the combination of the broad costal and subcostal areas and the extension of CUP to about half the wing length, the anal area being very long and slender.

Heteroptilon, new genus

Fore wing: costal margin smoothly curved; wing broadest beyond the middle of the wing; RS with 4 primary branches; CUA with a distal fork; anal veins unbranched.

Type-species: *Heteroptilon costale*, n.sp.

The generic name is derived from the Greek words *heteros* (different) and *ptilon* (wing) and is considered neuter and singular.

Heteroptilon costale, n.sp.

Figure 8

Fore wing: length, 15 mm; width 5 mm. Costal area with about 12 veinlets; RS with 5 terminal branches; M1+2 unbranched, M3+4 forked to half its length. Cross veins as shown in figure 8.

Holotype: no. 5878, Museum of Comparative Zoology. This consists of a complete fore wing, very well preserved. The cross veins, excepting those in the costal area, are very faint. The wing membrane is irregularly wrinkled, giving the impression that it was very thin.

The venation of this insect presents no difficulty in interpretation. R1 and CUA are strongly convex, and between them are two neutral veins (\pm), obviously RS and M. I have interpreted the most posterior branch that arises from the stem RS as R4+5 but this could also be regarded as an anterior branch of M, coalesced with RS basally.

There are several unusual features of this insect. The costal and subcostal areas combined are about half the width of the entire wing, the configuration of the costal area itself is most peculiar, and the crowding of the anal veins into the elongate anal area is unique among the Protorthoptera as presently known. The position of the family in the order is therefore uncertain.

ORDER PALAEODICTYOPTERA

This order, although a prominent one in the Upper Carboni-

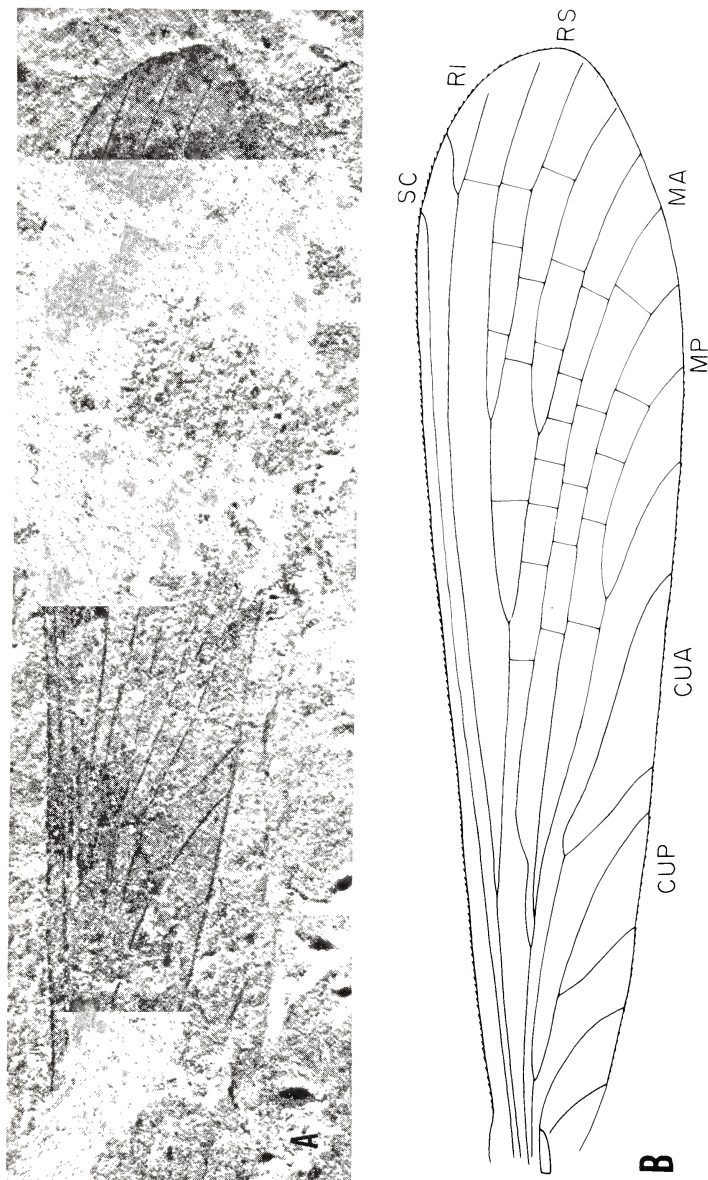


Figure 9. *Elmohoria piperi*, n.sp. A, photograph of holotype, no. 5839ab, M.C.Z. This is a composite photograph of the obverse and reverse combined. Length of wing, 15 mm. B, drawing of forewing, based on holotype.

ferous, is only sparsely represented in Permian strata. Two species have been reported from the Elmo beds.³ One of these, *Dunbaria fasciipennis* Tillyard, is a typical spilapterid. The other, *Kansasia pulchra* Tillyard, was originally described as a spilapterid (Tillyard, 1937) but has subsequently been transferred by Demoulin (1954) to the extinct order Archodonata. Although incompletely known, *pulchra* is almost certainly closely related to the species on which the order Archodonata was based (Martynov, 1931), but I do not believe that any of these insects are sufficiently distinctive to justify separation from the Palaeodictyoptera. Accordingly, I consider the Archodonata to be synonymous with the Palaeodictyoptera.

Among the fossils which I collected at Elmo in 1927 is a specimen that shows both palaeodictyopterous and megasecopterous traits. No additional specimens of this insect have subsequently been found, but I am now quite convinced that it is a representative of a new family of Palaeodictyoptera.

Family **Elmoboriidae**, new family

Fore wing: slender, at least four times as long as wide. Costal margin nearly straight; SC long, terminating a short distance before the wing apex; R1 close to and nearly parallel to SC, except distally; RS arising about $\frac{1}{4}$ wing length from base, with several branches; M forking nearly at the same level as the origin of RS; MP forking almost immediately after its origin, with 2 or 3 branches; CU forking near the base of the wing; CUA and CUP deeply forked; at least 2 anal veins. The costal margin of the wing is conspicuously serrate, the posterior margin less so. Hind wing and body unknown.

This family differs from others previously described in the Palaeodictyoptera by the elongate shape of the wing, which is broadest distally, and by the proximity of the forking of M to the first fork of MP. The family is based on the genus *Elmoboria*, described below; the genus *Oboria* Kukalova (1960), from the Permian of Moravia, apparently belongs here also.

³A third species, *Permoneura lameerei*, was doubtfully placed in the Palaeodictyoptera (Carpenter, 1931) but as pointed out below (p. 373) the unique specimen on which the species was based does not show the diagnostic features of the order.

Elmoboria, new genus

Fore wing: R1 extending almost to wing apex; RS dichotomously branched, with 4 terminal branches; MA arising slightly basad of the origin of RS, unbranched; MP3+4 deeply forked.

Type-species: *Elmoboria piperi*, n.sp.

The generic name is a combination of the names of the towns Elmo, in Kansas, and Oboria, in Moravia, both of which have important insect-bearing deposits of Permian age. The name is considered feminine and singular.

Elmoboria piperi, n.sp.

Figure 9

Fore wing: length, 15 mm; maximum width, 3.2 mm. Branches of RS about equal in length; shortly after its origin MA abruptly curves towards RS. The wing is traversed by three distinct bands of dark pigmentation and has a smaller spot nearer the base. The weak cross veins can be discerned only with difficulty.

Holotype: No. 5839ab, M.C.Z., collected at the Harvard quarry in Elmo in 1927. This consists of a complete wing, very well preserved. The distal part of the wing is on one piece of rock and the basal portion on its counterpart; photographs of these two pieces have been combined together in figure 9A to show the complete wing. The specimen is presumed to be a fore wing but since the shape of the wing is unusual for a palaeodictyopteron, we have no basis for evaluating the differences between the fore and hind wings in this new family. The insect has been placed in the Palaeodictyoptera because of (1) the remoteness of R1 from SC and the

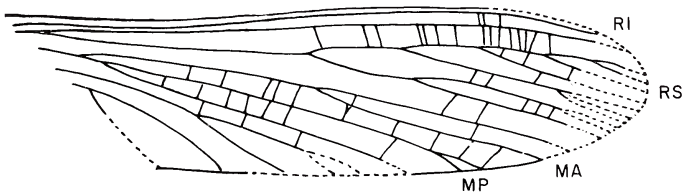


Figure 10. *Oboria longa* Kukalova, from Lower Permian of Moravia; drawing of fore wing, from Kukalova, 1960, with restoration of wing base omitted.

costal margin, (2) the wing shape, and (3) the presence of a 3-branched MP, which to my knowledge does not occur in the Megaseoptera, except for some of the highly specialized and aberrant Megaseoptera recently described by Kukalova-Peck (1975). However, the difficulty of distinguishing between the wings of the Megaseoptera and Palaeodictyoptera prevents any certainty in this assignment (see Carpenter 1963 and 1967, and Kukalova-Peck, 1975).

The species is named for the late Charles Piper of Hope, Kansas, who for more than forty years has owned the property in Elmo on which the Harvard quarry has been located, and who consistently encouraged us and assisted us in the collecting of the fossils.

The genus *Oboria* Kukalova (1960) from the Lower Permian of Moravia, originally placed in the family Spilapteridae, apparently belongs to the Elmoboriidae. The species (*longa*) on which *Oboria* was based is known from a single wing, lacking the basal and distal portions (figure 10). In view of the structure of the complete wing of *Elmobia*, I think it most probable that the wing of *longa* had a more extended base than that which Kukalova reconstructed. If that were so, the wing would have been shaped much as in *piperi*. The general venational patterns in both species, the weak and irregular cross veins, and especially the proximity of the

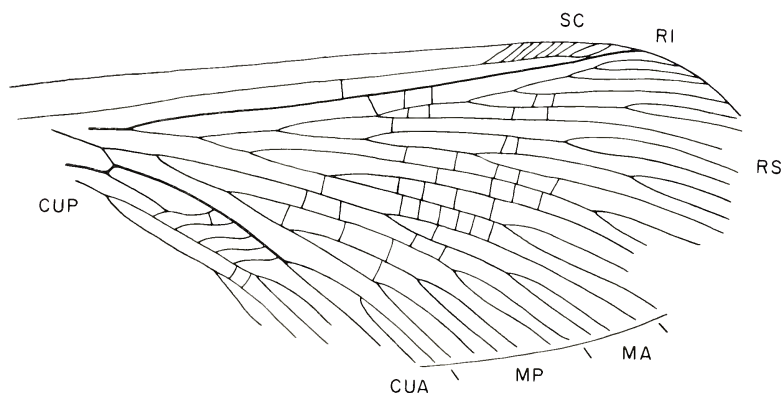


Figure 11. *Elmothone martynovae*, n.sp.; drawing of fore wing, based on holotype, no. 5585, M.C.Z. Length of wing, as preserved, 13 mm.

origin of MA to the fork of MP are indicative of family relationship. *Oboria*, however, differs from *Elmoboria* in having a more extensively branched RS and a deep fork on MA.

ORDER NEUROPTERA

The three suborders of Neuroptera (Sialoidea, Raphidioidea, and Planipennia) are first found in Permian deposits. The Planipennia have the most extensive record of the suborders in that period, with representations by three families and eleven genera. All of these Permian fossils are from the Soviet Union and/or Australia and most are from Upper Permian beds. However, specimens of two species have been described from Lower Permian deposits in the Kuznetsk Basin of the Soviet Union, although their precise position in the Lower Permian has not been determined. Until now these specimens have comprised the oldest record of the Planipennia.⁴

In the Museum of Comparative Zoology there is an incomplete wing of an ithonoid planipennian collected at Elmo in 1927. The hope of finding better specimens has deterred me from describing it over these many years, but since no additional fossils have turned up, I have decided to include a formal description of the species here. Inasmuch as the Elmo beds are part of the Lower Permian (Sumner Group), this new planipennian is at least as old as the Kuznetsk fossils. It clearly belongs to the Permithonidae.

Family Permithonidae Tillyard

Permithonidae Tillyard, 1922, p. 289; Martynova, 1961, p. 476. Synonyms: Permegalomidae Martynova, 1952, p. 201; Permopsychopsidae Riek, 1953, p. 82.

Fore wing: costal area moderately broad; costal veinlets numerous, somewhat irregular, some branched; SC terminating on RI distally or connected to it by a short cross vein; few to many cross

⁴Tillyard (1932, 1937) placed three genera of insects from the Elmo beds in the Planipennia but all have now been recognized as belonging to other orders: one (*Permobiella*), to the order Caloneurodea, and the other two (*Permoberothena* and its synonym, *Dictyobiella*), to the order Glosselytrodea (Martynova, 1962a). The latter order, although originally considered to be orthopteroid, is almost certainly closely related to the Neuroptera (Carpenter, 1964; Sharov, 1966).

veins between R and RS; RS with at least 4 primary branches; MA not coalesced with RS basally but often connected to it by a short cross vein; CUA with a distinct fork. Hind wing and body unknown.

This family is known from the Upper Permian of USSR and Australia.

Elmothone, new genus

Fore wing: costal margin straight, nearly parallel to SC; wing apex apparently broadly rounded. Costal area not as broad as in other known genera of the family; RS forking shortly after its origin and having at least 7 primary branches. M (and MA) remote from RS, forking shortly beyond the origin of RS, and with at least 7 subsequent forks; CU remote from M basally but CUA at its origin directed sharply towards M and connected to it by a short cross vein; CUP ending in a long, sigmoidal cross vein; the rest of the area between CUP and 1A having several other sigmoidal cross veins. 1A deeply forked. Cross veins in general weak and irregularly distributed.

Type-species: *Elmothone martynovae*, n.sp.

The generic name is derived from Elmo, the name of the township in Kansas in which the insect beds are located, and the generic name *Ithone*, which is feminine.

Elmothone martynovae, n.sp.

Figure 11

Fore wing: length (as preserved), 13 mm; maximum width, 5 mm; R1 very nearly straight; posterior branch of M with 4 subsequent forks. Venational details are shown in figure 11.

Holotype: No. 5585ab, Museum of Comparative Zoology.⁵ This consists of an incomplete wing, lacking about the basal quarter and part of the hind margin. The longitudinal veins, for the most part, are clearly preserved but the cross veins are indistinct, except under oblique light. The relatively narrow and uniform width of the costal area is suggestive of a hind wing. However, the hind wings are entirely unknown in the Permithonidae, and the struc-

⁵This is the fossil mentioned by MacLeod in his account of the Neuroptera of the Baltic amber (1970, p. 147).

ture of MA in *Elmothone* is not like that of the hind wings of the Ithonidae, to which the Permithonidae are apparently closely related. For this reason I consider the type of *martynovae* to be a fore wing.

The species is named for Dr. Olga Martynova of Moscow, who was on the staff of the Paleontological Institute for many years and is the author of numerous publications on fossil insects and Recent Neuroptera, Trichoptera and Mecoptera.

The genus *Elmothone* seems closest to *Permithonopsis* and *Permegalomus*, from both of which it is distinguished as follows: In *Elmothone* SC does not (apparently) terminate on R1, as has been described and figured for the other known genera of the family, although it almost touches R1 and is joined to it by a short cross vein; this is the situation in the Ithonidae. The structure of CUA in *Elmothone* is also very different from that of the other genera. In *Permithonopsis* and *Permegalomus* CUA nearly touches M but in *Elmothone* it is remote from M, although joined to it by a relatively long cross vein. Also, the area below CUA is unusually wide and is traversed by several sigmoidal cross veins. A suggestion of this condition occurs in *Permorapisma*, another member of the Permithonidae.

It is worthy of note that the Permithonidae were quite small insects, only about half the size of the existing members of the family Ithonidae.

FAMILIES OF UNCERTAIN ORDINAL POSITION

The insects described or discussed below are unusual in various respects and I have been unable to place them with confidence in any known order. Two of the species, *Permembia delicatula* Tillyard and *Permoneura lameerei* Carpenter, have already been formally described; the others, obviously belonging to very different orders, whatever they might be, are new. Having had these specimens for the past fifty years without coming to definite conclusions on their systematic positions, I have decided to describe and name them without making ordinal assignments. Related fossils present in collections from other Permian beds may ultimately be correlated with these Elmo fossils.

These "incertae sedis" insects belong to five very distinct families:



Figure 12. *Trachopteryx martynovi*, n.sp.; photograph of holotype, no. 7497, M.C.Z. Length of wing, as preserved, 13 mm.

1. Family **Trachopterygidae**, new family

Small insects. Fore wing: coriaceous; veins thick, the membrane very rough or rugose. Costa marginal, unusually thick, extending to apex of wing; the rest of the wing margin also thick, but less so; venation reduced, with all veins (except SC and possibly 1A) arising from a main stem-vein and extending in almost straight lines diagonally across the wing. Cross veins absent on most of the wing. Numerous fine setal bases on the costa and most other veins.

Trachopteryx, new genus

Fore wing: SC short, crowded between the costa and the stem-vein and terminating at about the level of the origin of MA. The other seven main veins (as interpreted below) are long but without branches.

Type-species: *Trachopteryx martynovi*, n.sp.

The generic name is derived from the classical Greek words *trachys* (rough) and *pteryx* (wing) and is considered feminine and singular.

Trachopteryx martynovi, n.sp.

Figures 12 and 13

Fore wing: length, 11 mm; width, 5 mm. RS arising about $2/3$ the wing length from the base; R1 with 4 short cross veins leading

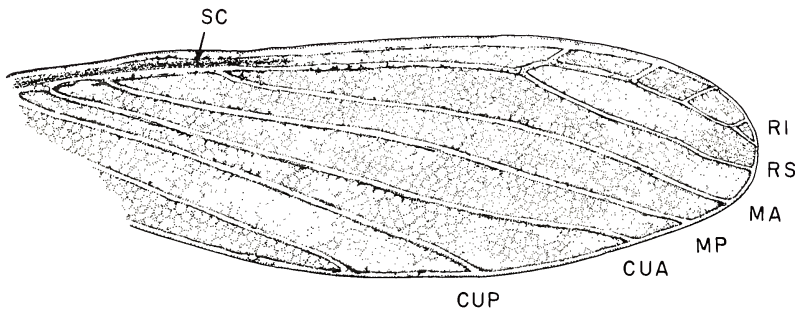


Figure 13. *Trachopteryx martynovi*, n.sp.; drawing of wing, based on holotype. Length of wing, as preserved, 13 mm.

to the costal margin beyond the origin of RS; MA arising at about 1/3 the wing length from the base; origins of CUA and CUP close together; termination of CUA directed apically, away from CUP. The rugosity of the wing membrane is shown in figure 12.

Holotype: no. 7497, M.C.Z., collected at Elmo, 1927. The species is named for Dr. A. V. Martynov, whose field and laboratory studies on Paleozoic and Mesozoic insects of Russia, from 1922 to 1937, initiated the extensive research program in paleoentomology now being carried out by the Academy of Sciences of the Soviet Union.

As shown in the photograph (figure 12), the holotype consists of a very well preserved wing, lacking only a small piece of the posterior margin near the base. The most obvious features of this wing are the origins of most of the veins from a common stem, and the strongly rugose nature of the wing membrane.

The interpretation of the venation presented in figure 13 seems to be the most logical one, although others are possible. The convexities and concavities of the veins are distinct in the unique type, which consists of only one counterpart, the other being missing. In this specimen the main stem-vein continues as R; since this is concave, I consider this counterpart to be the reverse half, the convexities and concavities being the reverse of those as they appear on the dorsal surface of an insect's wing. In the following discussion and in figure 13 reference is made to the veins as they would appear in the reverse half.

The subcosta extends only about as far as the origin of MA and is contiguous with both C and the stem-vein; it can be discerned only with difficulty because of the rugosity of the wing membrane. The main stem-vein is convex; beyond the origin of MA the vein appears to be a normal radius (R), with an anterior branch (R1) and the posterior RS. The four remaining veins that arise from the stem, alternately convex and concave, are presumably MA, MP, CUA and CUP. The origin of the most posterior vein, 1A, is uncertain; it may arise independently or from the stem-vein.

This is a highly specialized wing and I can make no convincing suggestions regarding its ordinal affinities. So far as I am aware, none of the Neoptera have an MA which is actually convex, as in this fossil, but that *Trachopteryx* is paleopterous seems hardly credible.

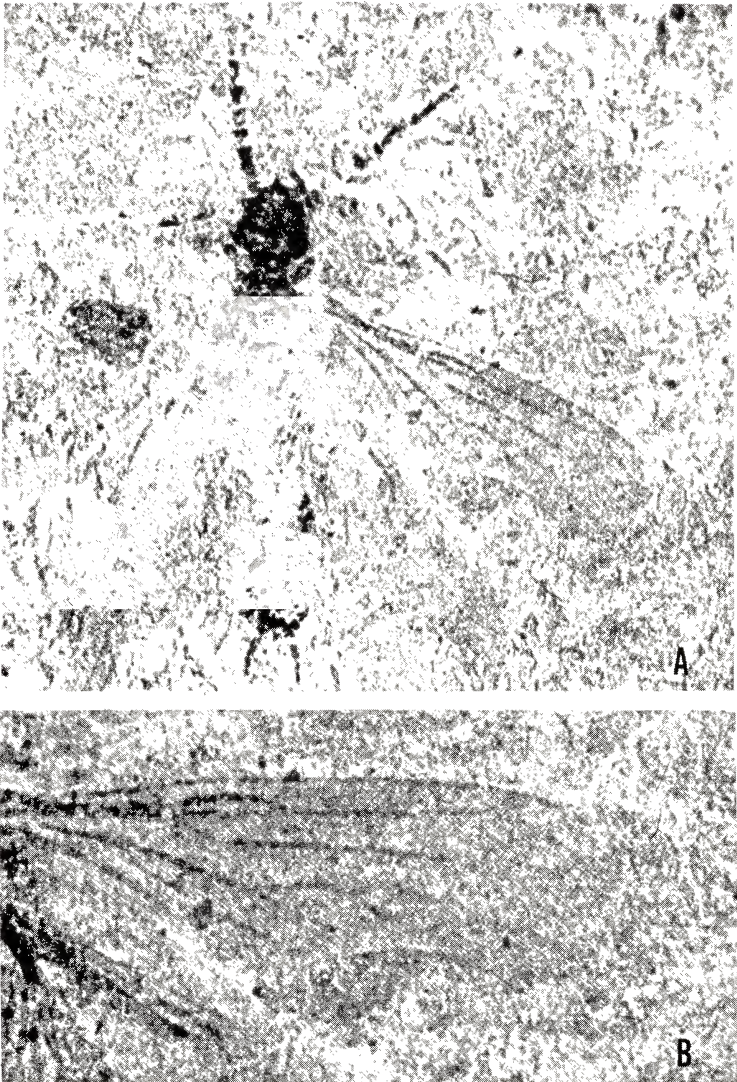


Figure 14. *Permambia delicatula*. A, photograph of holotype, no. YPM5403, Peabody Museum, Yale University. B, photograph of fore wing of type. Length of wing, 2.8 mm.

2. Family Permembaliidae Tillyard

Permembaliidae Tillyard, 1937, p. 92.

In 1928 Tillyard described, as a new genus and species, *Permembra delicatula*, a very small insect that he placed in the family Delopteridae Sellards (1909). Convinced that this family was related to the Psocoptera [Copeognatha], he transferred the Delopteridae from the Protorthoptera, where it had been assigned by Sellards, to the Psocoptera, within a new suborder, Embiopsocida. Subsequently (1937) Tillyard erected the new family Permembaliidae for the genus and also placed there the new genus *Nugonioneura*. The affinities of both these genera have remained obscure. *Nugonioneura*, now better known than previously, has been shown above to belong to the Protorthoptera, but *Permembra* still remains a mystery.

Martynov, in 1930 and unknown to Tillyard, had already placed the family Delopteridae in synonymy with the family Palaeomantidae Handlirsch (1906) and had designated the Palaeomantidae as representative of a new order, Miomoptera (1927).⁶ Subsequent studies of additional material have confirmed Martynov's conclusion on the synonymy of these families and have tended to support the recognition of the Miomoptera as a distinct, though poorly defined, order. In 1962, Martynova in a general survey of the order Miomoptera also placed the family Permembaliidae there, but with

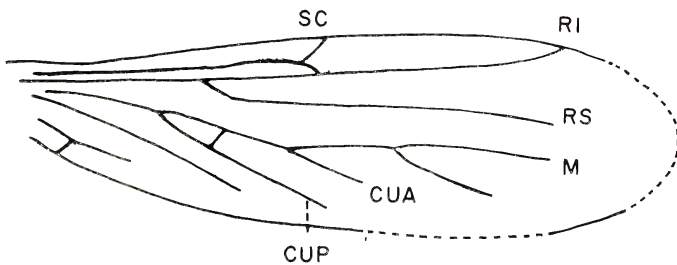


Figure 15. *Permembra delicatula*. Drawing of fore wing, based on holotype. Length of wing, 2.8 mm.

⁶For an account of the nomenclatural complexities involved in the designation of this taxon, see Carpenter, 1935, p. 105.

some uncertainty. The problem of *Permembia* results from lack of venational details in the unique specimen of *delicatula*, the species on which the genus was based. The difficulty is determining the actual, as opposed to the possible, characteristics of the genus and the family.

Dr. Kukalova experienced this in connection with her study of the Delopteroidea and other Miomoptera from the Permian of Moravia (1963). Using a photograph of the type of *delicatula* that I had sent her, she concluded that Tillyard had incorrectly described and interpreted the venation, which she considered more like that of the Delopteroidea than Tillyard thought. She also placed in the Permembiiidae two new genera of Miomoptera (*Permonika* and *Permonia*) from Moravia.

I have given much thought to the problem of *Permembia* since its original description and have repeatedly studied the type of *delicatula* at the Peabody Museum, Yale University, with the hope of finding some useful details previously overlooked. Only recently have I come to the conclusion that specimens of this insect are present in the Harvard collection also, though they are identifiable mainly on the basis of body structures, the venation in all specimens being more poorly preserved than that of the type. Our interpretation of the relationships of *Permembia* must therefore continue to rest for the time being on the venation of that specimen. From my examination of it, I am now convinced that Tillyard's interpretation of the venation was correct in all but minor details and that the genus *Permembia* (and of course the family Permembiiidae) cannot logically be assigned to the order Miomoptera.

The type of *delicatula* (no. YPM5403, Peabody Museum) consists of a nearly complete insect, as shown in figure 14A. One fore wing is spread out but the other three wings are folded or twisted in such a manner that their venation is not discernible. The head is relatively large and distinctly triangular in shape, markedly broad posteriorly, not globular as figured and described by Tillyard. The compound eyes are protuberant and situated posteriorly, as shown in the photograph. I certainly do not discern the three ocelli shown by Tillyard. The mandibles and palpi are not distinctive but the antennae are surprisingly thick and robust; the segments, numbering about 13, are as broad as long and subequal.

The thorax is relatively broad, the mesothorax being the largest segment. The abdomen, showing 10 distinct segments, terminates in a pair of short, segmented cerci. Several other small terminal processes, about 0.2 mm in length, are visible, but their nature is not obvious.⁷ The fore wing, which is only 2.8 mm long, was obviously very delicate and thin; this is indicated by the folded and twisted condition of the other wings of the type and of all of the wings of the specimens in the Harvard collection. The drawing of the wing of the type shown in figure 15 includes only those veins which I am confident can be seen by anyone who studies the specimen. The enlarged photograph of the wing in figure 14B shows most, if not all, of these veins. The wing is not narrowed basally as much as depicted by Tillyard. The proximal and middle parts of the wing are well preserved, especially considering the minute size of the insect, but the distal region and part of the posterior area are either broken away or simply not preserved. SC is distinct and terminates on R1 at about mid-wing. R and R1 form a straight line up to nearly the termination of R1, which is well before the apex of the wing. RS arises about 1/3 the wing length from the base and is nearly straight, diverging slightly away from R1; it is not preserved beyond the end of the level of R1 and I am unable to see any sign of its wide distal fork depicted by Tillyard or of the several branches which Kukalova mentions as probably present. M arises independently of R but apparently coalesces basally with CU; CUP diverges away first, with M+CUA continuing until near mid-wing, where M diverges anteriorly and soon forks. M is not preserved beyond the end of R1, which prevents our knowing whether or not other forks were present. Similarly, CUA is not preserved as far as the wing margin, but it is unbranched as far as it can be traced. 1A and 2A are incomplete, without branches. I have been able to distinguish only three cross veins with certainty, as shown in the figure: between SC and the costal margin, between CUP and M+CUA, and between 2A and the hind margin of the wing. I have no doubt that other cross veins were present in the wing, but I am concerned here with those that I believe can

⁷Tillyard was of the opinion that the asymmetry of these minute appendages suggested relationships with the Embioptera but in my experience most small processes on insects are asymmetrical when preserved in fossils, as a result of the softening of the cuticle.

clearly be seen. There are several features of this wing as interpreted here that resemble those of the fore wings of the Miomoptera, such as the form of SC and the coalescence of CUA with the stem of M. However, these are also features that are commonly found in many orders of insects. More important, I believe, is the apparent absence of two characteristics which occur in all known Miomoptera: the presence of 2 or 3 branches on RS and of a deep, prominent fork on CUA. Although neither RS nor CUA in the type of *Permembra* is preserved completely to the wing margin, there does not seem to be sufficient space remaining for the characteristic branching.

Rather than modify the diagnosis of the Miomoptera to accommodate *Permembra*, it seems preferable to place the genus in *incertae sedis* at the ordinal level (probably within the orthopteroid complex) until specimens showing complete fore and hind wings have been found.

Five specimens which appear to belong to this species are in the Harvard collection: nos. 7526ab, 7539ab, 7547, 7596, and 7474. All show the characteristic head shape and other body features, including the robust antennae, but in all specimens the wings are badly twisted and folded.

In this connection it is appropriate to mention *Sheimia sojanensis* Martynova (1958) from an Upper Permian deposit at Sheimo-Gora, Kuloy River Basin, Arkhangelsk Region, Soviet Union. This minute insect, with a wing-length of about 4 mm., is known only

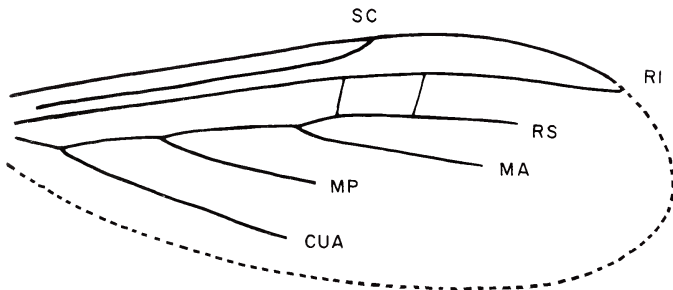


Figure 16. *Sheimia sojanensis* Martynova, from Permian of Sheimo-Gora, Arkhangelsk Region, USSR; drawing of fore wing, based on holotype, no. 1145/117, Paleontological Institute, Moscow. Length of wing, 3 mm.

by the poorly preserved holotype, which has been loaned to me for study by the Institute of Paleontology in Moscow. The general form of the body and the structure of the antennae in particular are like those of *Permembra*, but the wing venation is so different that at least family separation seems necessary. My interpretation of the venation is like that of Martynova's (1962) in most respects. However, I cannot discern the short vein that she has identified as CUP, or the vein posterior to it in her figure; and I see no trace of the basally oblique vein which her figure shows extending from R to the M+RS complex. My concept of what can definitely be seen in this wing is shown in figure 16. Although there are similarities to the venation of *Permembra*, there is one very significant difference: the absence in *Sheimia* of a free RS arising independently from R. For this reason, I do not believe that *Sheimia* can be considered at all closely related to the Permembriidae, in spite of the apparent similarities in body structure.

Martynova was of the opinion that *Sheimia* was a member of the order Embioptera and she designated a separate suborder (Sheimiodea) for it, a view that was subsequently followed by Riek (1970, p. 179). For my part, I do not believe that there is enough evidence for an embiopteran position of this fragmentary fossil to justify extending the range of the Embioptera from the Oligocene (their present earliest record), back to the Permian — an interval of about 190 million years. There is certainly no indication in the specimen of *S. sojanensis* of the thickened blood sinus (R1), or of the enlarged fore basitarsi, or even of a generalized venational pattern that might have led to that of the existing order Embioptera. It seems to me preferable, therefore, to assign the family Sheimiidae to *incertae sedis* at the ordinal level within the orthopteroid complex until additional and better preserved specimens of *Sheimia* have been found.⁸

3. Family **Apheloneuridae**, new family

Very small insects, with fore and hind wings similar, but not identical, in both size and venation. Fore wing: SC ending on

⁸I have recently examined about thirty specimens of insects, comparable in size to *Sheimia sojanensis* and from the same deposit, but none of them are even remotely related to the Sheimiidae.



Figure 17. *Aphelonera minutissima*, n.sp. Photograph of holotype, no. 7527, M.C.Z. Length of fore wing 3 mm.

costal margin at about mid-wing, also unbranched; M independent from R, with three long branches; CU dividing into CUA and CUP at wing base; CUA with a long anterior branch (CUA1) almost parallel to hind margin of wing and terminating near wing apex; CUA2 shorter; CUP nearly straight, short. Hind wing: slightly shorter than fore wing; venation similar but CUA unbranched. Cross veins weakly developed in both wings, but numerous and apparently small; antennae slender and relatively long, with many segments.

The most striking feature of this family is the nearly parallel arrangement of R, M1+2, M3, M4, and CUA1, especially in the fore wing, and the lack of branching on these veins beyond mid-wing.

Apheloneura, new genus

Fore wing: RS arising at about 1/5 of wing-length from the base; M1+2 forking about mid-way between the levels of the origins of RS and the forking of M3+4; CUA arising from CU very close to wing base. Hind wing: M1+2 arising much nearer the forking of M3+4 than to the origin of RS.

Type species: *Apheloneura minutissima*, n.sp.

The generic name is derived from the classical Greek words *aphel* (parallel), and *neura* (veins); the name is considered plural and feminine. Two species of the genus are in the M.C.Z. collection.

Apheloneura minutissima, n.sp.

Figures 17-19

Fore wing: length, 3 mm; width, 1 mm. Hind wing: length, 2.7 mm; width, 1 mm. The venational features of the holotype are shown in figure 19. CUA2 forms a straight line with the stem of CUA, and it is deeply forked.

Holotype: no. 7527, M.C.Z.; collected at Elmo in 1927. This specimen (figure 17) has all four wings, parts of the antennae, and obscure portions of the thorax and abdomen. The preservation of the fossil is remarkable considering its small size. The longitudinal veins are to be seen without difficulty, but the cross veins can be distinguished only under oblique lighting along the wing

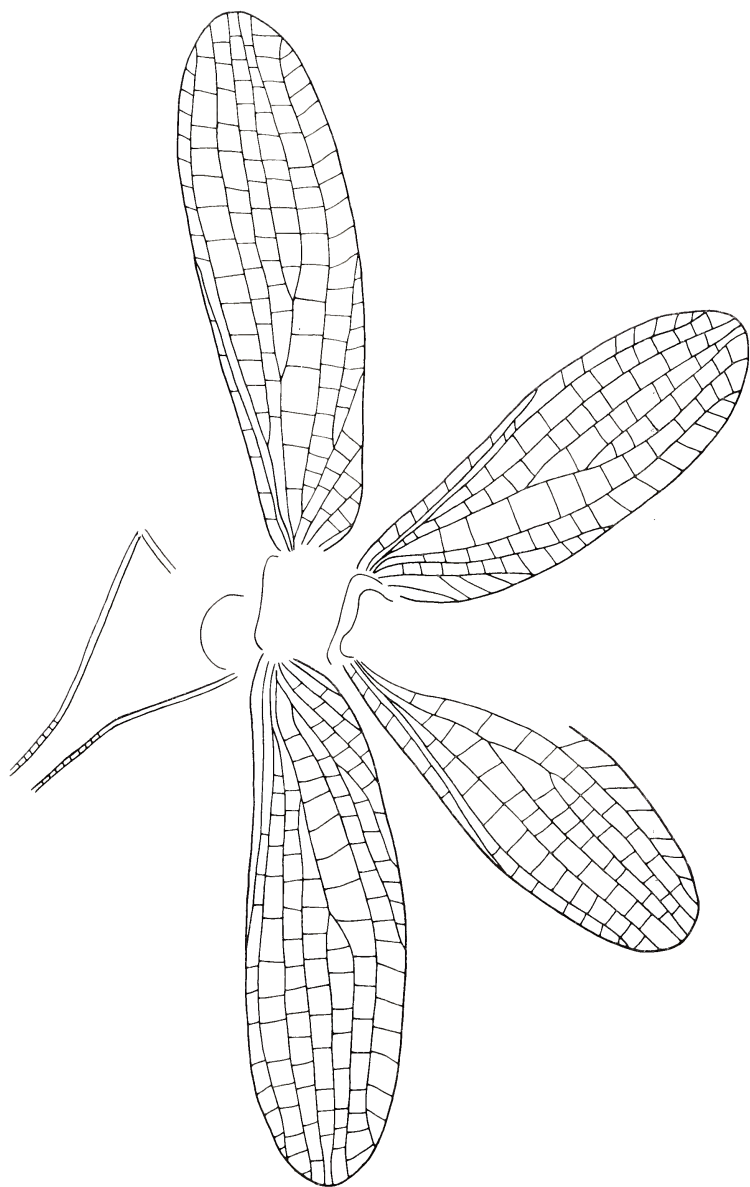


Figure 18. *Apheloneura minutissima*, n.sp.; drawing of holotype.

axis. The body is poorly preserved, showing only portions of the thorax and abdomen, and an irregular structure anterior to the mesothorax that probably consists of a small pronotum and the head, although details are not preserved. Arising from the head region is one antenna (1.2 mm long); the other antenna, although broken away from the head region, is more clearly preserved for a greater length (2.2 mm). The segments of the antennae that are visible are about twice as long as broad.

Paratype: no. 7533ab; collected at Elmo in 1932. This consists of a less clearly preserved specimen than the holotype, with one fore wing outstretched, and the others overlapping the abdomen and each other. The fore wing is 2.8 mm long and 1 mm wide. One antenna is preserved for 1 mm, and its segmentation is like that of the holotype.

In addition there is one other specimen in the collection: no. 7534, with the wings overlapping the abdomen; the fore wings are 3 mm long.

***Apheloneura amplia*, n.sp.**

Figure 20

Fore wing: length, 4.8 mm; width, 1.5 mm. Venation similar to that of *minutissima*, but RS arises somewhat nearer the wing base, CUA2 is unbranched, and CUA1 (not CUA2, as in *minutissima*) continues the straight line of the stem of CUA. Cross veins are preserved in several areas of the wing, much as in *minutissima*. The hind wing (partially preserved in paratype 7525) is apparently like that of *minutissima*.

Holotype: no. 8604 M.C.Z., collected in 1927. This consists of a very well preserved fore wing.

Two other specimens, not designated as types, are in the collection, as follows: no. 7525, showing the thorax, abdomen, and basal parts of all four wings, with the structure of CUA very clear; no. 7522, a more poorly preserved specimen with all wings overlapped.

This species is conspicuously larger than *minutissima*. The presence in the collection of three specimens, all of them of the larger size and all having the same structure of CUA1 and CUA2, shows that these are not simply over-sized specimens of *minutissima*.

I have not yet been able to reach any conclusion about the ordinal position of the Apheloneuridae. There are two obvious

features of their wings: the reduction of branches on most longitudinal veins, and the similarity of the fore and hind wings. Each of these traits has appeared quite frequently in various orders of insects, but their combined occurrence is very infrequent, at least among Recent groups. The most obvious instance is the Embioptera — which is why *Permembra* and *Sheimia*, among others, have been regarded as their close relatives. However, there are no

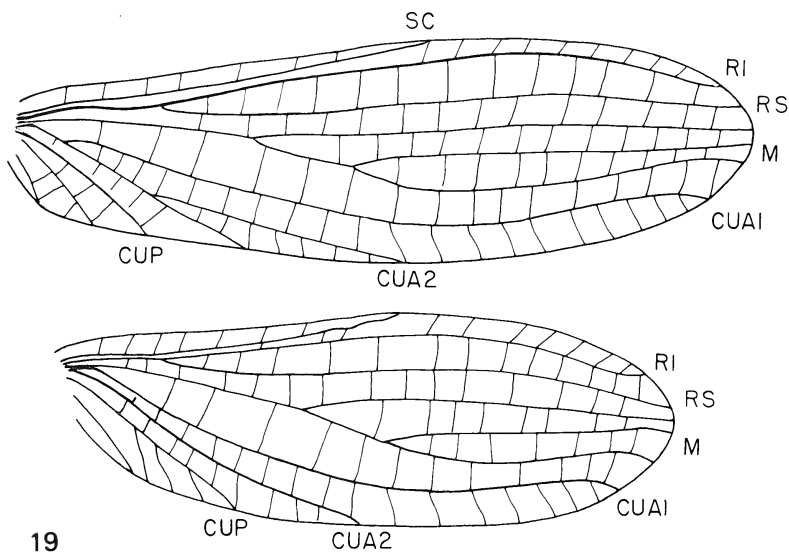


Figure 19. *Apheloneura minutissima*, n.sp.; drawing of fore and hind wings, based on holotype. Length of fore wing, 3 mm.

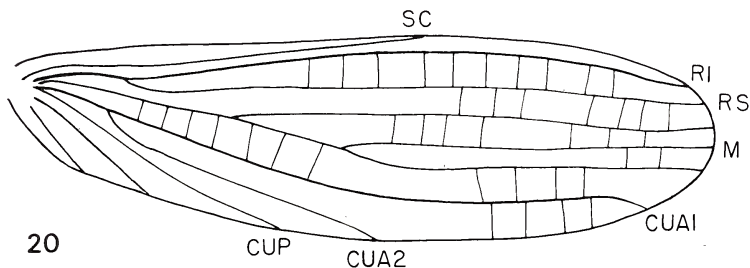


Figure 20. *Apheloneura amplia*, n.sp.; drawing of fore wing, based on holotype, no. 8604, M.C.Z. Length of fore wing, 4.8 mm.

venational details of the Apheloneuridae that suggest to me their close relationship with the Embioptera. It does seem probable, though, that the order has ultimately been derived from some aberrant protorthopterous stock, and the Apheloneuridae may well have been among the early, distant relatives of that stock.

The fore wings of *Apheloneura*, in fact, have a venational pattern much like that of the Permian Probnisidae (Protorthoptera), with the branches of RS and M reduced and CUA extending nearly to the wing apex. However, the probnisid hind wings are typically orthopterous, with a large and expanded anal fan and a distinctive venation, unlike that of the fore wings. It is the hind wing of the Apheloneuridae that induces me to withhold the family from the Protorthoptera and to place it in *incertae sedis*.

In this connection it should be noted that the Apheloneuridae are not the only Permian insects having subequal wings that show orthopteroid relationships. The Miomoptera, for example, which have a distinctive venational pattern and which are very abundantly represented in Permian beds, are in this category. There are, in fact, many similar insects, about the size of Permembidae and Apheloneuridae occurring in the Permian of Kansas, Oklahoma, and the Soviet Union, all of which are apparently orthopteroid but show remarkable diversity of structure. These have not yet been formally described, mainly because they are not clearly preserved. Until more of these small insects are better known, I believe it is advisable to leave the Apheloneuridae, along with the Permembidae and Sheimiidae, in the category of "order unknown".

4. Family **Gelasopteridae**, new family

Insects of moderate size. Fore wing: very long and slender; SC ending on costa beyond mid-wing; R1 extending very nearly to apex of wing; RS unbranched, M forked beyond mid-wing; CUA diverging at its origin towards M and connected to it by a short cross vein (or possibly a branch of M); then continuing without branches to near the apex; CUP and IA unbranched; cross veins numerous, mostly straight. Hind wing: about as long as fore wing. Body slender, prothorax elongate.



Figure 21. *Gelasipteron gracile*, n.sp.; photograph of holotype, no. 7511ab, M.C.Z.. Length of fore wing 28 mm.

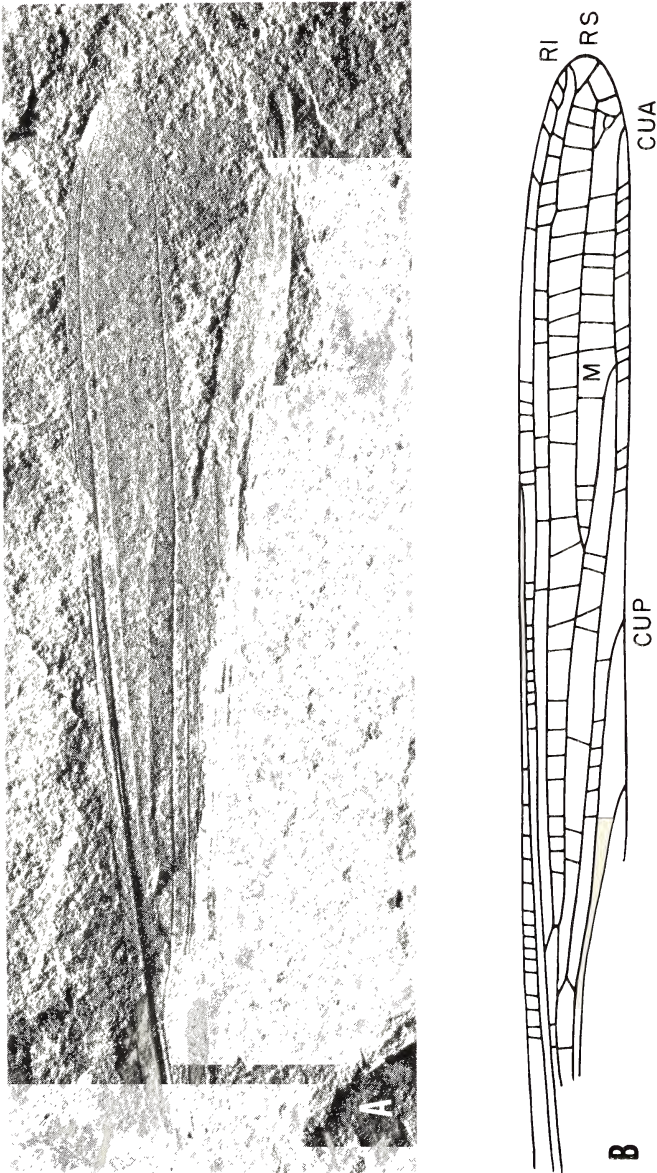


Figure 22. *Gelasopteron gracile*, n.sp. A, photograph of fore and hind wings of holotype. B, drawing of fore wing of holotype. Length of fore wing, 28 mm.

Gelasopteron, new genus

Fore wing: about ten times as long as wide; costal area only of moderate width basally; RS arising at about 1/6 wing length from base, continuing straight and parallel to R1 for its entire length; anterior branch of M weak, terminating obscurely near the wing apex; posterior branch of M terminating on CUA.

Type-species: *Gelasopteron gracile*, n.sp.

The generic name is derived from the classical Greek words *gelastos* (ridiculous) and *pteron* (wing) and is considered neuter and singular.

Gelasopteron gracile, n.sp.

Figures 21–22

Fore wing: length 28 mm (as preserved); width 2.8 mm; estimated complete length, 30 mm. Costal margin very straight up to the apical region; base of the costal area not preserved; R1 mostly straight, curving posteriorly at the apex, as it parallels the costal margin; M forking the level of the termination of SC, the anterior branch about twice as long as the posterior one.

Holotype: no. 7511ab, M.C.Z.; collected at the Harvard quarry at Elmo in 1927. This specimen consists of a nearly complete wing and parts of others, as well as fragments of the thorax and abdomen. As shown in the photograph (figure 21), one fore wing is stretched out at right angles to the body; a second wing of the same length, presumably the hind wing of the same side, partially overlaps the fore wing basally and is twisted and rotated so that its hind margin is contiguous with the hind margin of the fore wing. The distortion of the hind wing prevents a satisfactory study of its venation; the apical part appears to be like that of the fore wing. However the long CUA, the predominate feature of the fore wing, does not seem to be present in the hind wing, and there is a suggestion of an anal fan that has been folded up under the rest of the wing.

The two wings on the opposite side of the thorax are flexed along the body, both of them folded and twisted together. The apical part (about 7 mm, labeled AP in figure 21) is bent at an acute angle to the rest of the wing, which is 20 mm long.

Little is preserved of the body. A small portion can be seen posterior to the base of the wing; this is about 6 mm long and 2

mm wide. The posterior third of this portion seems to be the first abdominal segment, but there is nothing preserved beyond that. The body anterior to the wings, presumably the prothorax, is about 10 mm long up to the edge of the piece of rock containing the specimen. This part seems to be 4 mm wide, i.e., about twice as wide as the posterior part, but about half of that width seems to consist of a pair of femora that extend along the sides of the prothorax.

The general picture derived from this curious fossil is of an insect with a long prothorax and abdomen, and with extremely long and slender fore wings, perhaps with an anal fan on the hind pair. There is some suggestion in this of a phasmatodean, but the venation of the fore wing has virtually nothing in common with that of the Triassic and Jurassic Phasmatodea described by Sharov (1968). Comparison with existing Phasmatodea is difficult since none, so far as I am aware, have normal or fully developed fore wings.

My assumption is that *Gelasopteron* is a member of the orthopteroid complex, in spite of the unbranched RS; but we will need to wait for more fossil evidence before removing the insect from the *incertae sedis* category.

5. Family Permoneuridae

Permoneuridae Carpenter, 1931, p. 124; Tillyard, 1937, p. 87; Laurentiaux, 1953, p. 425.

This family was established for *Permoneura lameerei* from the Elmo beds and placed, with some doubt, in the order Palaeodictyoptera. The unique specimen on which this species was based consisted of a single wing, which I assumed to be a hind wing because of its broad anal area. Two features of this wing were unusual: the pectinate branching of RS and the apparent anastomosis of MA with the basal branch of RS for its entire length. A third feature, the absence of CUA, was unknown in the Palaeodictyoptera.

Many different opinions have been expressed about this insect since its description. Tillyard (1937) was of the opinion that *Permoneura* was a very highly specialized offshoot of the ancestral stock of *Dunbaria* and that the loss of CUA might have been due

to abnormal development of the unique specimen on which the species was based. His final suggestion was that *Permoneura* be placed in the Spilapteridae, near *Dunbaria*. Laurentiaux (1953), on the other hand, placed it in a new order, Permoneurodea, close to the Palaeodictyoptera. Rohdendorf (1962) assigned it to the order Archodonata, which in my opinion is inseparable from the Palaeodictyoptera. Dr. Kukulova-Peck has suggested (personal communication) that the type of *lameerei* might be a hind wing of a protorthopteron. This is indeed a possibility, but none of the Protorthoptera are known to have a pectinate RS in the hind wings and none are known to lack CUA.

Inasmuch as no additional specimens of *Permoneura* have turned up in the 45 years since its description, I believe the family Permoneuridae should be placed in the category of *incertae sedis* at the ordinal level. This has the advantage of removing it from both the Palaeodictyoptera and the Protorthoptera, in neither of which it seems to belong. Its assignment to a separate order of its own seems unjustified; an order based on a single wing has no meaning.

Reexamination of the specimen of *lameerei* convinces me that although my original figure is essentially correct (1931, figure 6), it does not indicate that all the veins are concave, except for R and R1 and, apparently, the short basal piece of MA. A photograph of the counterpart of this specimen, showing the peculiarity of the venational topography, is included here (figure 23).



Figure 23. *Permoneura lameerei*; photograph of holotype, no. 9876, M.C.Z. Length of wing, 9 mm.

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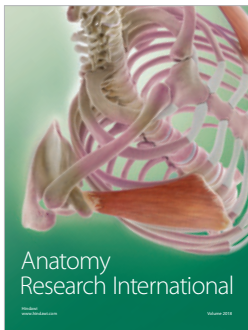
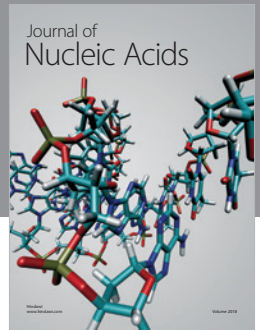
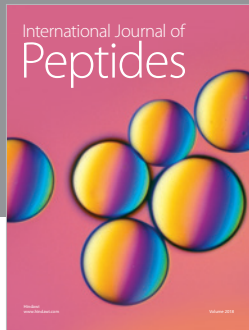
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