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KANSAS PERMIAN INSECTS.
PART 18. THE ORDER EMBIARIA.

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ABSTRACT.

This paper deals with the only true Embiid so far found in the Kansas Lower Permian beds, viz. *Protombia permiana* n. g. et sp. For this archaic type a new Suborder Protombiaria is proposed and also a new family Protombiidae. The evolution of the Order Embiaria is discussed and the existing genus *Clothoda* is indicated as standing nearest to the new fossil. As the female of the fossil species possessed an ovipositor and large compound eyes, it is concluded that it was not a web-spinner to the extent that recent forms are: (the fore tarsi are missing).

In shaping up a rather large piece of rock on which were impressed the scattered remains of several larvae of the Order Protoperlaria, I was fortunate enough to uncover the first specimen of an undoubted member of the Order Embiaria so far discovered in the Kansas Lower Permian beds. This specimen, No. 15507*a-b*, lies on the extreme edge of a small piece of rock about one and one-half inches long, which I broke off from the larger slab mentioned above and then split open into two parts, each a little more than one-quarter of an inch thick. The surface of the rock is slightly rough and uneven, so that the impression of this very delicate insect is not as good as we might wish. Nevertheless, it is clear enough for the insect to be accurately determined and for many of its parts to be made out.

The specimen appears to be undoubtedly a female, owing to the shape of the abdomen and the presence of what appears to be a small ovipositor. Nevertheless, it is fully winged, whereas all existing types within this Order have the females wingless. The head is well preserved, the compound eyes being much larger than in recent types. The hindwings, unfortunately, lie across the fore at a slight angle, thus making

the determination of the venational scheme one of considerable difficulty, especially as the veins are very light and not easy to follow. The combination of characters shown by this unique specimen undoubtedly requires the erection of a new suborder and family for its reception.

In working out the wing-venation, it is necessary to emphasize two points: firstly, that the venational scheme, even if a single wing had been available, would have been very faint and not easy to interpret, and, secondly, that, as the fore and hindwings on each side overlie one another to a considerable extent, the veins crossing at acute angles, the interpretation of the middle portion of the venation is doubly difficult. In attempting to reconstruct the complete venation of the forewing, which is clearer than that of the hind, I worked first of all on the basal and apical portions which are free from the overlapping of the hindwing. In the basal portion, six free veins can be seen, of which the two most anterior arise together; these are interpreted as Sc, R, M, Cu, 1A and 2A. The fourth vein, Cu, becomes fairly strong and convex a little way from the base, and gives off a posterior branch, which is clearly CuP. The first and second veins, Sc and R, diverge slightly, and R itself becomes a strong convex vein; it can be followed to nearly half-way along the wing length, where it passes across the costa of the hindwing. The origin of Rs can just be made out near this point. The distal course of Sc is not at all clear, and I am not quite certain whether it actually ends up on the costa or merely ceases to be chitinized before reaching it.

In studying the apical portion of the forewing, seven distinct veins can be seen, ending at approximately equal intervals along the distal border. The first of these is evidently R_1 . The next two can be followed back in one wing to a common stem, and should therefore be R_2 and R_3 , as shown in Fig. 3. These veins, and the four following them posteriorly, are all weakly chitinized and flattened out; in some places it is possible to pick up, very faintly, a line of faint dots indicating the bases of insertion of macrotrichia along these distal veins. As far as these can be made out, they appear to have arisen along, or very near, the anterior margins of the flattened veins. I have therefore, in Fig. 3, indicated this formation by adding a dotted line anterior to the continuous line marking the course of each vein.

The exact positions of the forks of Rs and R_{4+5} are very obscure and do not appear to agree in the two pairs of wings.

The positions given in Fig. 3 must be taken as only approximate. The same is true to some extent of the course of M and the position of its fork. The forking of CuA also does not appear to be the same in both wings; as there appears to be a fairly distinct indication in one wing of an extra branch, I have indicated this in Fig. 3 by a broken line.

Suborder PROTEMBIARIA subordo nova.

Both sexes fully winged. Compound eyes large, placed laterally, wide apart. An ovipositor present in the female. Cerci multi-articulate.

Family PROTEMBIIDAE, fam. nov.

Prothorax moderately large, divided by a transverse groove into two parts. *Mesothorax* longer than wide, subrectangular. *Metathorax* slightly shorter than wide. *Legs* very short, the tarsi about half as long as the tibiae. *Wings* long and slender, with complete venation. Rs four-branched; M two-branched; CuA either two- or three-branched; CuP a separate, complete vein. Two anal veins present. Distal parts of veins Rs and M flattened out and carrying macrotrichia along their anterior margins. *Abdomen* in female fusiform, somewhat broader in middle than thorax, the ten segments distinct, though segments 1 and 2 are shorter than the rest. *Ovipositor* short, V-shaped.

Genus PROTEMBIA n. g.

(Figs. 1-3.)

With the characters of the family, to which may be added the following:—

Forewing four times as long as wide, somewhat narrowed basally, the costa gently curved, the posterior margin very nearly straight, the apex moderately rounded. Sc faint but distinct, apparently ending weakly on costa at about two-thirds from base. R₁ a fairly strong vein, nearly straight, but curving upwards distally to meet the costa well before the apex. Rs arising a little before half-way, diverging strongly from R₁ and soon forking into two branches, each of which is again forked before it reaches the distal margin; R₂₊₃ forks at about the level of the end of R₁, R₄₊₅ well before this. M is a faint vein but appears to be distinct from R right from the base of the wing; it runs with a slight curve below R₁ and Rs and

forks distally into two near the level of the fork of R_{4+5} . Cu forks close to base of wing; CuA is a strong vein and forks into two at about one-third of the wing length; in one forewing there are indications of an extra distal fork, indicated in

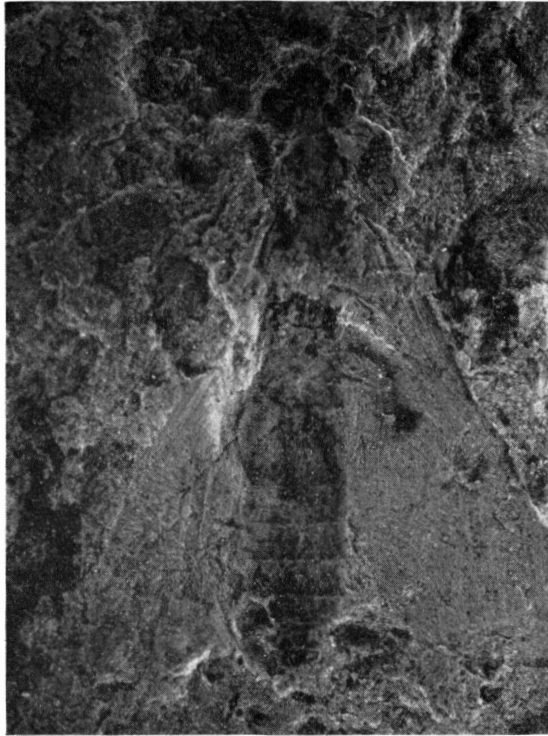


Fig. 1. *Protombia permiana* n. g. et sp. Photograph of holotype reverse. Specimen No. 15507b ($\times 11$).

Photo by W. James.

Fig. 3 by a broken line; CuA_1 reaches the posterior margin at about two-thirds of its length, CuA_2 at about one-half; CuP is a straight vein, very weakly chitinized, ending up not far from CuA_2 , to which it converges distally. The anal area is narrow and carries two veins, 1A and 2A, diverging slightly and placed about equidistantly between CuP and the anal margin.

Genotype:—*Protombia permiana* n. sp.

Horizon:—Lower Permian of Kansas.

PROTEMBIA PERMIANA n. sp.

(Figs. 1-3.)

Total length of body 7.3 mm.; length of forewing 6.2 mm., breadth of same 1.5 mm.

The obverse impression (15507a) shows the body more clearly than the reverse, but is, unfortunately, broken off just beyond the seventh abdominal segment. Fig. 2 has been drawn mainly from the obverse specimen, with the last three segments of the abdomen added from the reverse specimen.

The head is fairly clearly marked, 1 mm. wide, the large compound eyes placed antero-laterally, the clypeus and labrum projecting anteriorly. The ocelli are apparently absent. The

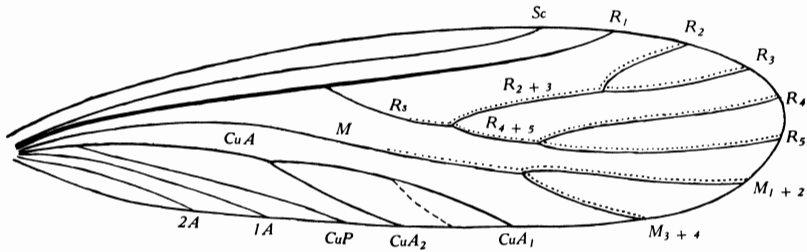


Fig. 2. *Protambia permiana* n. g. et sp. Holotype obverse. Specimen No. 15507a, with most of wings omitted. Length of body 7.3 mm. *ant* antenna, *cr* portion of cercus, *e* compound eye, *fw* basal part of forewing, *hw* basal part of hindwing, *ov* ovipositor, *ps* posterior margin of left hindwing, partly overlapping abdomen, *T*₁ prothorax, *T*₂ mesothorax, *T*₃ metathorax, 1-10 the ten abdominal segments.

antennae are inserted slightly inwards and anteriorly to the eyes: about nine moniliform segments of the right antenna are visible, and two or three, less distinct, of the left. Two deeply impressed, curved lines, symmetrically placed, run through from the region of the prothorax on to the head, and appear to represent the margins of a strongly developed *gular plate* and *mentum*, impressed through from the ventral surface; there is a squarish patch of dark pigment lying between them at the narrowest part.

Thorax:—The *prothorax* has the lateral margins convex, and is somewhat narrowed anteriorly; it is not as wide as the head. The narrower anterior portion appears to be divided off from the broader posterior part by a definite transverse groove. The *mesothorax* is the largest segment of the body;

it is about 1 mm. long and 0.8 mm. wide; its antero-lateral margins are slightly rounded. The *metathorax* is shorter and narrower than the mesothorax, about 0.6 mm. long by 0.7 mm. wide. All three segments of the thorax have indications of a

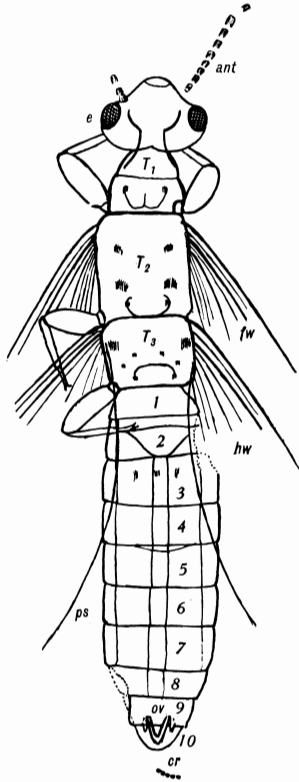


Fig. 3.

Fig. 3. *Protembia permiana* n. g. et sp. Forewing, restored. Actual length 6.2 mm. Amended Comstock-Needham notation for veins: CuA, first cubitus (convex) with its two main branches CuA₁ and CuA₂; CuP, posterior cubitus (concave).

small posterior sclerite, which I interpret as the *sternellum* showing through from the ventral side.

The *legs* are short and placed wide apart. The fore legs are inserted laterally well back on the prothorax; they are poorly preserved in both obverse and reverse specimens, but show a

stout femur projecting outwards and forwards and a slender tibia turned inwards so that its distal end and the whole of the tarsus are hidden beneath the head of the insect. Hence it is impossible to state the number of tarsal segments, nor can we tell whether the tarsi had the first segment swollen, as in recent Embiaria, or not. The middle legs are inserted right at the hinder lateral angles of the mesothorax; the femur is stout and fusiform, the tibia slender and about as long as the femur, the tarsus short, about half as long as the tibia; again, it is impossible to make out the number of tarsal segments. The hind legs are inserted similarly at the hinder lateral angles of the metathorax, and appear to have been closely similar to them; in the obverse specimen, the tibia is turned inwards so that its distal part and the tarsus lie across the left side of the first abdominal segment.

Wings:—In both obverse and reverse specimens, the outlines of the wings can be faintly seen impressed upon the rock, lying just clear of the body and at an acute angle to it, the hindwings lying at a somewhat greater angle to the body than the fore, and hence also crossing the forewings obliquely at a slight angle and therefore masking to a considerable extent the middle portion of the venation. In the reverse impression, the wings are complete on both sides, but very faint; in the obverse, the apical portions of the left pair are missing owing to a break in the rock. The venation of the forewing is much clearer than that of the hind. In outline, the forewing is an elongate oval, the breadth being only one-fourth of the length. The outline of the hindwing is a somewhat shorter and wider oval, with the posterior margin much more distinctly curved.

The venation has already been fully described in the definition of the genus; that of the forewing is shown in Fig. 3. There are very faint indications of cross-veins here and there on the wing; but, as I am quite unable to allocate these between the two wings, they are omitted in Fig. 3. There is also a very faint indication of granulation of the wing-membrane in the distal part of the wing, which may possibly indicate the presence of numerous microtrichia on the membrane itself.

The *abdomen* is long and slender, fusiform in shape, indicating that the specimen was a female. Its greatest width, on segments 3-7, is somewhat wider than that of the thorax, but allowance must be made for flattening down of the softer abdomen during the process of fossilization. Segments 1 and 2 are short and slightly narrower than the succeeding segments;

segments 3-7 are all wide, about three times as wide as long; segments 8-10 are shorter and gradually taper to a bluntly rounded end. Projecting from segment 9 is a hard, dark, symmetrically V-shaped structure which appears to have been a reduced ovipositor. Some little way beyond the end of the abdomen, in the reverse impression, there can be seen a series of four or five very small, subcylindrical segments which evidently belonged to the *cerci*; these latter, therefore, must have possessed a number of small segments and could not have been similar to the two-segmented cerci of recent *Embiaria*.

Types:—*Holotype obverse*, Specimen No. 15507a, and reverse, No. 15507b, in Yale University Collection. The reverse is a practically complete specimen, but the obverse, which is somewhat better preserved, has the last three segments of the abdomen missing and also the apical portions of the left pair of wings, owing to a break in the rock.

Evolution of the Order Embiaria.

The new genus *Protombia*, though it is undoubtedly a true Embiarian, stands far apart from the other known members of the Order. It is unfortunate that we cannot be certain about some of the more important characters, notably the number of segments in the tarsi, the structure of the first segment in the fore tarsus, certain details of the venation, etc., but the fossil is well enough preserved for us to obtain a fairly good idea of its principal characters.

One of the most interesting characteristics of the Order *Embiaria* is the web-spinning habit. Although, unfortunately, we are not able to discover from our new fossil whether the genus *Protombia* was a web-forming type or not, there are several considerations which lead me, for one, to consider that it most probably was not. Firstly, if the first segment of the fore tarsus had been anything like as swollen as in recent forms, I think that its impression would have been shown in the fossil even though the tarsus happened to lie below the head. I have carefully followed the two fore tibiae in the fossil beneath the borders of the head capsule, and I am not able to distinguish anything that appears to be a globular swelling just beyond them. Again, there are certain characters which appear to be correlated with the web-spinning habit; these are, in recent forms, the loss of wings in the female, the loss of the ovipositor, and the reduction in size of the compound eyes. Therefore it seems reasonable to suppose that a form in which

the female was fully winged and possessed an ovipositor and large compound eyes was most probably not a web-spinner,—at any rate, not to the extent that recent forms are.

The multi-articulate cerci are of great interest. Most recent forms have the cerci biarticulate, though very rarely the left cercus may be reduced to a single segment. In the females, the cerci are always symmetrical. In the males, they are symmetrical in the most archaic genus, *Clothoda*, but become asymmetrical in all other genera, where they play a part in the formation of the peculiar, asymmetrical, copulatory apparatus. Hence it seems reasonable to conclude that the cerci in *Protembia* must have been entirely symmetrical in both sexes, and that the course of evolution was, firstly, a reduction to two segments in both sexes, and, secondly, asymmetry. Thus, on this character, *Clothoda* would stand between the primitive multi-articulate stage and the most highly developed asymmetrical types now existing.

Turning to the wing-venation, we can say with considerable certainty that there does not appear to be a single venational character in which *Protembia* could not be the direct ancestor of all recent types of Embiaria. We may note the following points:

(1) The subcosta, Sc, is longer and more complete than in recent forms, in all of which it either ends up blindly at about half-way (*Clothoda*) or else is very short and ends blindly in the costal space at a quarter or a third of the wing-length.

(2) The radial sector, Rs, has more branches than in any recent forms. In almost all the genera of the family Embiidae, Rs is three-branched, and we note that it is R_{2+3} which is simple, R_{4+5} being branched. This is what would be expected if reduction of the distal branches were to take place, for the fork of R_{2+3} is shorter and more distally placed in *Protembia* than that of R_{4+5} . The movement backwards towards the base of the point of origin of Rs on R, in recent forms, can be correlated with the reduction of Sc and the narrowing of the costal and subcostal spaces, whereby R_1 and Rs respectively tend to occupy the positions originally held by Sc and R_1 . There is a parallel type of evolution of these veins in the Blattoidea.

We should note that the genus *Calamoclostes* (fam. Embiidae, South America) has four branches to Rs in the hindwing. The fork of R_{2+3} is, however, very short, and one wonders whether it is a constant for the genus, or only an individual variation. The forewing of this genus, in the only figure

known to me, has, curiously enough, a radial sector with only two branches!

(3) The media, M, is two-branched, as in *Donaconethis*, where also there is no basal connection between Rs and M. In *Clothoda* and other recent genera, M is simple and is connected with Rs basally by a short cross-vein, forming an *arculus*.

(4) The first cubitus, CuA, is branched, apparently only two-branched, though there is an indication of an extra branch apically in the reverse impression. The wide fork of CuA resembles rather closely that of most modern genera. In the forewing of *Clothoda*, however, CuA is shown with three branches, whereas the hind has only two. The extra branch in this genus may not, of course, be constant, especially as it is absent in the hindwing. Bearing in mind, however, that the forewing, in this Order, has apparently always been longer and narrower than the hind, there does not seem to be any valid reason why the original form of CuA in the forewing may not have possessed a very wide fork, in which an extra branch may easily have been developed. As the cubitus is not at all clear in the fossil, this point cannot be decided with certainty.

(5) The second cubitus, CuP, is quite distinctly chitinized. In recent forms, it appears to have degenerated into a faint groove, with little or no chitinization.

(6) There are two anal veins, quite distinct. Recent forms possess only one, and that quite a short vein.

(7) The venation in general, though faint, is distinctly chitinized, whereas in recent forms there is always more or less degeneration of the actual veins, only R_1 remaining at all well chitinized.

Reviewing the above evidence, it would seem clear that *Protombia*, both on its venational and other characters, may be accepted as the actual ancestor of existing types. The nearest (and therefore the most archaic) of existing genera is *Clothoda*, which, on the primitive character of possessing an undivided tenth tergite in the male and symmetrical genitalia, should, in my opinion, be placed in a separate new family Clothodidae. *Donaconethis* has also preserved one character, the forked media, not found in any other living genus, but in other respects is so close to the rest of the family Embiididae that it should be retained in that family.

We can now offer the following complete classification of the Order Embiaria:

Suborder PROTEMBIARIA subordo nova.

Embiaria winged in both sexes, with large and prominent compound eyes, cerci multiarticulate, female with a small ovipositor.

Family 1 PROTEMBIIDAE. Rs four-branched, M and CuA both branched. Only a single genus, *Protombia* n. g. Lower Permian of Kansas.

Suborder EUEMBIARIA subordo nova.

Embiaria wingless in the female, winged or wingless in the male; compound eyes of medium size, morulate, often prominent; cerci with two segments, more rarely one only. Recent or Tertiary forms.

Key to the Families of the EUEMBIARIA.

1. Genitalia symmetrical in the male, the tenth tergite undivided
Fam. CLOTHODIDAE n. fam.
(A single genus, *Clothoda*, from Africa.)
Genitalia asymmetrical in the male, the tenth tergite divided
into two hemitergites.....2.
2. Rs three-branched in one or both wings; female with first
abdominal sternite fully developed.....Fam. EMBIIDAE.
(Genera *Donaconethis*, *Calamoclostes*, *Rhagadochir*, *Embia*,
Ptilocerembia, *Haploëmbia*, *Monotyloa*.) (Tropical and
subtropical.)
Rs two-branched in both wings; female with first abdom-
inal sternite obsolescent.....Fam. OLIGOTOMIDAE.
(A single genus, *Oligotoma*, cosmopolitan.)

CANBERRA, AUSTRALIA.